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Classification et relations entre les traits fonctionnels des crustacés zooplanctoniques : de l'organisme à l'écosystème

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Classification et relations entre les traits fonctionnels des crustacés zooplanctoniques : de l'organisme à l'écosystème

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Abstract

Ecologists have long recognized that organisms are sustained by the flux, storage and turnover of ecosystem energy, which fuels biological metabolism, and material, used to construct biomass. Over the past three decades, the importance of individual organisms in regulating ecosystem processes, such as consumer-driven nutrient cycling, has been increasingly recognized. Occupying a central position in aquatic food webs, zooplankton are known to influence other trophic levels and exert a strong influence on energy fluxes or material processing in ecosystems. Several species' characteristics have been pointed out as being good indicators, or predictors, of the effect of zooplankton on their environment, including individual body size, corporal stoichiometry and specific physiological rates. Most of these characteristics can also be termed "functional traits". While the use of traits has recently gained popularity amongst aquatic community ecologists, few have applied this approach to concretely link zooplankton community structure to ecosystem processes. In the present study, we compiled data from a wide variety of literature to construct a database of crustacean zooplankton species and their traits contributing directly or indirectly to C, N or P ecosystem fluxes. Our literature search yielded over 9000 empirical observations on 287 different species and thereby allowed identification of knowledge gaps in the literature. We explored trait relationships amongst taxonomic units and between marine and freshwater habitats. Of all cross-correlations tested among 16 zooplankton traits, 35 were significant, with most traits being related to body mass. Our synthesis revealed significantly different patterns between freshwater and marine zooplankton respiration and allometry (body mass vs. length). We propose a novel trait classification scheme according to both organismal and ecosystem functions. Our goal is to provide a database for zooplankton functional traits, tools to link organisms to ecosystem processes, and to promote a search for general patterns and trade-offs amongst traits.

Keywords: allometry, biogeochemical cycles, body size, ecosystem functioning, functional traits, metabolism, nutrient recycling, zooplankton.

Résumé

Les écologistes reconnaissent depuis longtemps que les organismes sont soutenus par le flux, l'emmagasinage et le renouvellement d'énergie et de matériel de l'écosystème, puisqu'ils sont nécessaires au métabolisme biologique et à la construction de biomasse. L'importance des organismes dans la régularisation des processus écosystémiques est maintenant de plus en plus considérée. Situé au centre des chaînes trophiques aquatiques, le zooplancton influence les flux d'énergie et de matériel dans les écosystèmes. Plusieurs de leurs caractéristiques sont connues comme étant de bons indicateurs de leur effet sur l'environnement, notamment leur taille, contenu corporel et taux métabolique. La plupart de ces caractéristiques peuvent être appelées « traits fonctionnels ». Alors que l'emploi des traits devient de plus en plus populaire en écologie des communautés aquatiques, peu ont su utiliser cette approche afin de concrètement lier la structure des communautés zooplanctoniques aux processus écosystémiques. Dans cette étude, nous avons colligé les données provenant d'une grande variété de littérature afin de construire une base de données sur les traits du zooplancton crustacé contribuant directement ou indirectement aux flux de C, N et P dans les écosystèmes. Notre méta-analyse a permis d'assembler plus de 9000 observations sur 287 espèces et d'identifier par le fait même ce qu'il manque à nos connaissances. Nous avons examiné une série de corrélations croisées entre 16 traits, dont 35 étaient significatives, et avons exploré les relations entre les unités taxonomiques de même qu'entre les espèces marines et d'eaux douces. Notre synthèse a entre autres révélé des patrons significativement différents entre le zooplancton marin et dulcicole quant à leur taux de respiration et leur allométrie (masse vs. longueur corporelle). Nous proposons de plus une nouvelle classification de traits liant les fonctions des organismes à celles de l'écosystème. Notre but est d'offrir une base de données sur les traits du zooplancton, des outils afin de mieux lier les organismes aux processus écosystémiques et de stimuler la recherche de patrons généraux et de compromis entre les traits.

Mots-clés : Allométrie, cycles biogéochimiques, fonctionnement de l'écosystème, métabolisme, recyclage des nutriments, taille corporelle, traits fonctionnels, zooplancton.

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Liste des abréviations

C:	Carbone / Carbon
N:	Azote / Nitrogen
P:	Phosphore / Phosphorus
NH_4^+:	Ammonium / Ammonia
PO_4^{3-}:	Phosphate
O_2:	Oxygène / Oxygen
CO_2:	Dioxyde de carbone / Carbon dioxide
PON:	Azote organique particulaire / Particulate Organic Nitrogen
DON:	Azote organique dissous / Dissolved Organic Nitrogen
MTE:	Théorie métabolique de l'écologie / Metabolic Theory of Ecology
EST:	Théorie stœchiométrique de l'écologie / Ecological Stoichiometry Theory
CIEE:	Institut d'écologie et d'évolution / Institute of Ecology and Evolution
ANCOVA:	Analyse de covariance / Analysis of Covariance
OLS:	Moindre carré ordinaire / Ordinary Least Squares
ln:	logarithme naturel / Natural Logarithm
BL:	Longueur du corps / Body Length
DM:	Masse sèche du corps / Dry Mass of the body
Ct:	Contenu corporel / Body Content
Ind.:	Individu / Individual

« Success is the ability to go from one failure to another with no loss of enthusiasm. »

-Winston Churchill

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Chapitre 1 : Introduction générale

I. Contexte général

Un des paradigmes les plus classiques de l'écologie repose sur l'interaction et l'influence mutuelle entre les organismes et leur environnement physique, chimique et biologique (Elton 1927; MacArthur, 1955; 1972). Que ce soit au niveau de l'individu, de la dynamique des populations ou des interactions à l'échelle des communautés, les organismes modulent les fonctions d'un écosystème via leur biomasse, métabolisme et comportement (Jones et Lawton, 1995; Rosenzweig, 1995; Chapin *et al*., 2000, Vanni, 2002; Enquist *et al*., 2003; Allen *et al*., 2005). Les fonctions écosystémiques, tels que le renouvellement, l'emmagasinage et les flux de carbone (C), d'azote (N) et de phosphore (P), ne sont donc pas seulement influencées par la présence et l'abondance d'une communauté, mais également par la structure de celle-ci (Balseiro *et al*., 1997; Schindler *et al*., 1997; Enquist *et al*., 2009).

Le terme ''fonction écosystémique'' est maintenant largement employé pour faire allusion aux propriétés, processus et services d'un écosystème. Afin d'illustrer clairement ce qu'on entend par les fonctions d'un écosystème, il est possible de catégoriser ses propriétés et ses processus en trois groupes : (1) le stock d'énergie et de matériel présents (e.g. biomasse, lot de nutriments), (2) les flux d'énergie et les transformations de matériel (e.g. productivité primaire ou secondaire, décomposition de matière, recyclage de nutriments) et (3) la stabilité des stocks et des flux dans le temps (Pacala et Kinzig, 2002;

Lecerf et Richardson, 2009). Quant aux services écosystémiques, ils dérivent essentiellement des propriétés et des processus qui, individuellement ou collectivement, représentent une source de bien-être pour les humains (Pacala et Kinzig, 2002). Le fonctionnement des écosystèmes est donc une combinaison de multiples fonctions écosystémiques.

Il n'en demeure pas moins que d'évaluer l'impact des communautés sur le fonctionnement d'un écosystème est un défi majeur et d'actualité en écologie (Grime, 1998; Loreau *et al*., 2001; Eviner and Chapin, 2003; Hooper *et al*., 2005). De ce fait, caractériser clairement une communauté représente une étape critique afin de pouvoir adéquatement lier la composition de celle-ci au fonctionnement de l'écosystème. Mis à part l'utilisation de mesures taxonomiques, la diversité d'une communauté peut s'estimer par la variabilité phénotypique, que celle-ci soit basée sur des différences régulées par la génétique ou bien induites par un changement dans l'environnement, conduisant par exemple à de la plasticité phénotypique. Ainsi, les caractéristiques phénotypiques, c'est-à-dire les traits des organismes, peuvent s'avérer être des attributs plus pertinents pour comprendre et prédire les relations espèce-écosystème que les indices taxonomiques, tel que le nombre d'espèces (Tilman *et al*., 1997; Walker *et al*., 1999; Norberg *et al*., 2001; Cadotte *et al*., 2009). Un des moyens nous permettant de saisir pleinement le rôle écologique des espèces présentes dans une communauté est l'utilisation de traits fonctionnels (Chapin *et al*., 1996; Lavorel and Garnier, 2002; Eviner and Chapin, 2003; Eviner, 2004).

II. L'approche par traits

Dans sa plus simple définition, un trait représente toute sorte de caractéristiques mesurables à l'échelle d'un individu, que celles-ci soient de nature morphologique, physiologique ou comportementale. Les traits sont souvent associés à la performance d'un organisme en vue d'optimiser son succès (ou *fitness*) par l'entremise de sa croissance, reproduction et survie (Darwin, 1859; Arnold, 1983; Geber et Griffen 2003; Reich *et al*., 2003). Ayant été initialement utilisés dans cette perspective évolutive, les traits font maintenant parties d'un cadre théorique intégrateur expliquant comment un changement dans les valeurs de traits sous des conditions environnementales fluctuantes peut influencer une panoplie de processus à plusieurs niveaux organisationnels, des individus aux écosystèmes (Violle *et al*., 2007). Ce type d'intégration est possible à travers le concept de « traits fonctionnels », soit tous ces traits ayant la capacité de nous informer sur les interactions entre les espèces ou entre celles-ci et leur environnement (Díaz et Cabido, 2001). En effet, ces traits peuvent être utilisés afin de représenter la dynamique d'une population (i.e. traits « démographique »; Saether et Bakke, 2000), d'exprimer la réponse fonctionnelle d'une communauté (traits « réponse »; McGill *et al*., 2006) ainsi que pour quantifier les apports provenant directement des organismes à l'échelle écosystémique (traits « effet »; Lavorel et Garnier, 2002). Cette perspective hiérarchique permet donc d'entrevoir différents types de traits, selon le niveau d'application ou d'implication, mais il n'en reste pas moins qu'ils sont tous mesurés au niveau de l'individu (Violle *et al*., 2007).

Certains types de traits présentent donc un fort potentiel d'impact sur les fonctions écosystémiques (i.e. traits « effet ») et sont particulièrement d'intérêt afin de pouvoir

extrapoler les effets des organismes à l'échelle de l'écosystème (McIntyre *et al*., 1999; Díaz et Cabido, 2001; Lavorel et Garnier, 2002; Eviner et Chapin, 2003). Quelques études ont d'ailleurs concrètement testé l'effet de certains traits (e.g. ceux de type physiologique (Calow, 1987)) sur des processus biogéochimiques, telle la productivité primaire ou la décomposition (Garnier *et al*., 2004; Kerkhoff et Enquist, 2006; Vile *et al*., 2006). Ainsi, le type et la nature d'un trait nous informent sur l'effet que les organismes peuvent avoir sur les fonctions écosystémiques, puis l'abondance relative des espèces qui partagent ces dits traits nous permet de prédire la magnitude que cet effet peut avoir.

Bien que l'approche par traits soit relativement bien implantée en écologie terrestre, elle n'est pas aussi fréquemment employée en écologie aquatique (Giller *et al*., 2004). De plus, les études ayant eu recours aux traits fonctionnels ont eu tendance à utiliser des traits plus facilement mesurables, ou plus communément accessibles dans la littérature, au lieu de se concentrer sur les traits étant plus directement liés aux fonctions écosystémiques qui leur étaient d'intérêt (Petchey et Gaston, 2006).

III. Le zooplancton

Dans les environnements aquatiques, le zooplancton est présent en forte biomasse et occupe une position pivot au centre des réseaux trophiques. Ces organismes sont donc des acteurs-clés dans les interactions trophiques et d'importants médiateurs d'énergie et de flux d'éléments dans les écosystèmes (Lampert *et al*., 1986; Elser *et al*., 1988; Sterner, 2009). Bien que certaines descriptions et classifications fonctionnelles ont récemment émergé en écologie des communautés zooplanctoniques (Barnett *et al*., 2007; Merico *et al*., 2009; Kiørboe, 2011; Litchman *et al*., 2013; Barton *et al*., 2013), la plupart de ces études

n'explorent pas les relations entre les traits de façon quantitative et ont tendance à omettre certains traits physiologiques connus pour influencer d'importantes fonctions écosystémiques, notamment le recyclage des nutriments. En effet, les traits considérés par ces études sont essentiellement liés à la performance de l'individu et aux interactions interindividuelles, laissant ainsi de côté des processus physiologiques d'intérêt majeur dans la régulation des flux d'éléments de l'environnement. Par exemple, les traits quantifiant la respiration, l'excrétion, le contenu des pelotes fécales ou qualifiant la capacité d'effectuer du *sloppy feeding* fournissent énormément d'informations sur le rôle du zooplancton au sein des cycles biogéochimiques, notamment celui de l'azote (Fig. IA) (Sirotnak et Huntly, 2000; Steinberg et Saba, 2008). La nature de la contribution du zooplancton à ces cycles varie donc selon l'effet qu'ont les traits dans le système et la magnitude de cet effet dépend de la taille de la population qui présente ces traits (Fig. IB). L'incorporation de traits physiologiques dans les classifications fonctionnelles est donc d'intérêt si l'objectif est de lier la composition des communautés aux fonctions de l'écosystème, particulièrement celles liées aux cycles de N, P et C.

Par le passé, diverses études se sont intéressées au métabolisme du zooplancton comme étant une fonction de la taille et/ou de la composition chimique de leur corps, sous conditions environnementales stables (Ikeda et Michell, 1982; Peters, 1983; Ikeda, 1985; Sterner, 1990; Sterner et Elser, 2002; Ikeda *et al*., 2001; Sereda et Hudson, 2011; Kiørboe et Hirst, 2014); cependant, ces relations ont rarement été examinées dans un contexte de diversité fonctionnelle. De plus, bien que les relations entre ces variables aient été

évaluées pour différents taxa, de différents habitats aquatiques, ces études restent à petite échelle et ne comparent pas les relations entre les traits à travers les écosystèmes.

i. Rôle du zooplancton dans les cycles biogéochimiques

Au cours des trois dernières décennies, l'importance du zooplancton dans les cycles biogéochimiques a considérablement été revendiquée, tant en milieu marin qu'en eaux douces (Elser *et al*., 1988; Sirotnak et Huntly, 2000; Vanni, 2002; Alcaraz *et al*., 2010). Leur rôle dans la biodisponibilité des nutriments et la régénération d'énergie s'effectue par plusieurs voies, que ce soit directement ou indirectement (Fig. II). Les effets directs proviennent essentiellement des transformations physiologiques entre le moment où les éléments sont consommés et celui où ils sont relâchés dans le milieu. Les éléments ingérés sont en partie assimilés par l'organisme, ce qui n'est pas assimilé sera relâché sous forme de pelotes fécales, puis ce qui est assimilé sera en partie utilisé pour l'approvisionnement ainsi que la croissance des tissus et l'excédent et les déchets métaboliques seront libérés via l'excrétion (Fig. II; Vanni, 2002). Les consommateurs zooplanctoniques influencent également le lot de nutriments indirectement en contrôlant la biomasse et la structure de communauté de leurs proies, modulant ainsi l'effet des maillons inférieurs sur les flux d'éléments (Sirotnak et Huntly, 2000; Vanni, 2002) (Fig. II).

Par sa prédation et les nutriments qu'il relâche dans l'environnement, le zooplancton exerce un contrôle bidirectionnel (i.e. descendant et ascendant ou *top down* et *bottom up*) sur la biomasse algale ainsi que sur les autres maillons inférieurs (Fig. III). En effet, l'excrétion de composés dissous par le zooplancton, sous forme d'ammonium (NH_4^+), phosphate (PO_4^3) et quelques composés organiques (acides aminés et urée)

(Lehman, 1980; Bidigare, 1983; Regnault, 1987), représente une source importante de nutriments biodisponibles pouvant fournir respectivement entre 19-130 % et 37-200% de la quantité de N et P nécessaire à la production primaire d'un système (Verity, 1985; Johnson *et al.*, 2010). Alors que l'excrétion est potentiellement la voie influençant le plus le lot de nutriments dissous, la respiration apparaît comme étant l'activité métabolique de base pouvant contribuer le plus au cycle du carbone en émettant du CO_2, considérant que ces deux processus physiologiques sont exercés par toutes les espèces de zooplancton (Mayzaud, 1973; Ikeda *et al*., 2001; Frangoulis *et al*., 2005; Alcaraz *et al*., 2010). La vitesse et la stœchiométrie auxquelles les espèces respirent et excrètent les éléments représentent donc des caractéristiques importantes afin de mesurer l'impact du zooplancton sur les flux de N, P et C dans leur écosystème.

ii. Équilibre stoechiométrique et théorie métabolique en écologie

De façon générale, le taux et la stœchiométrie d'une réaction métabolique représentent un centre d'intérêt très populaire en écologie, en partie grâce à la théorie métabolique (*Metabolic Theory of Ecology*; MTE) (Brown *et al*., 2004) et la théorie stoechiométrique (*Ecological Stoichiometry Theory*; EST) (Sterner et Elser, 2002). Le zooplancton a entre autres déjà été utilisé comme système d'étude pour tester et appliquer les modèles de ces théories (Ikeda, 1985; Sterner, 1990; Ikeda *et al*., 2001; Sterner et Elser, 2002).

Virtuellement, la plupart des processus métaboliques observés chez un organisme varient en fonction de leur masse corporelle à la puissance ¾, ou à l'exposant -¼ si le taux est rapporté par unité de masse (Kleiber, 1961; Peters, 1983; West *et al*., 1997; Gillooly *et*

al., 2001; Brown *et al*., 2004; West et Brown, 2005). L'explication amenée par la MTE a su rationaliser ce concept d'invariance énergétique en prenant également en compte la température du milieu (West *et al*., 1997; Brown *et al*., 2004). Explorer les relations entre les taux de respiration et d'excrétion en fonction de la masse des espèces de zooplancton, à température constante, permet ainsi de comparer la cinétique de ces processus physiologiques le long d'un gradient de taille et, par le fait même, d'évaluer l'effet indirect de la taille des organismes sur les flux de C, N et P dans le système. Ce type de modèle est particulièrement pertinent en vue d'évaluer les implications écologiques de la physiologie des organismes selon la structure de taille d'une communauté.

Par ailleurs, la stœchiométrie des produits excrétés par un organisme varie selon un principe de balance de masse. Le ratio élémentaire de l'excréta dépend essentiellement du déséquilibre entre le ratio du corps de l'organisme (i.e. ses besoins corporels) et le ratio de la nourriture ingérée. À valeur nutritive constante, EST prédit donc que plus les espèces présentent un ratio N:P élevé dans leur corps, plus celles-ci auront tendance à excréter des nutriments à un ratio N:P faible et vice versa (Sterner, 1990; Hessen et Andersen, 1992; Sterner *et al.*, 1992; Sterner et Elser, 2002). La composition élémentaire corporelle peut entre autres dépendre du contenu biochimique, c'est-à-dire de la nature et de la proportion des lipides et protéines; la composition biochimique peut également être utilisée afin de prédire la valeur du ratio N:P:O entre l'excrétion et la respiration (Ikeda et Michell, 1982).

Par le passé, le contenu chimique de plusieurs espèces zooplanctoniques a été analysé et une différence fondamentale dans le ratio corporel N:P a été détectée entre les principaux taxa de zooplancton. Ainsi, les daphniidés sont connues pour présenter un ratio

corporel N:P très bas, en raison de leurs besoins importants en P, comparativement aux autres cladocères, qui eux-mêmes sont connus pour présenter un ratio plus faible que celui généralement mesuré chez les copépodes (Andersen et Hessen, 1991; Elser et Urabe, 1999). Par conséquent, il est attendu que le ratio N:P de l'excréta des cladocères soit plus élevé (particulièrement celui des daphniidés) que celui des copépodes. Le ratio élémentaire N:P de l'excrétion est particulièrement d'intérêt lorsqu'il est comparé à celui du milieu, à savoir si celui-ci indique une limitation générale en N ou en P (i.e. supérieur ou inférieur à 16:1, Redfield, 1958). Ainsi, la variation du ratio N:P du contenu corporel et de l'excréta des espèces peut présenter d'importantes implications pour les processus écosystémiques, notamment la production primaire du système à travers différents habitats. Ces dits traits peuvent donc servir d'indicateurs, ou de prédicteurs, afin d'estimer la contribution du zooplancton au fonctionnement de l'écosystème.

IV. Objectifs d'étude

L'objectif global de cette étude est d'améliorer notre compréhension mécanistique de la structure des communautés zooplanctoniques et de fournir des outils permettant de mieux lier ces communautés au fonctionnement de leur écosystème. Nous focaliserons notre attention sur l'intérêt de l'approche par traits dans la caractérisation des communautés de zooplancton. Dans l'optique de mieux évaluer l'effet des crustacés zooplanctoniques sur les flux de N, P et C, nous avons effectué une méta-analyse à travers la littérature scientifique afin de compiler les valeurs de traits pouvant influencer directement ou indirectement ces flux, et ce, pour le plus d'espèces possible, tant en milieu marin qu'en eaux douces. Ainsi, nous avons colligé l'information sur les traits suivants:

taille corporelle (masse et longueur), composition chimique des espèces (C, N, P, ratio N :P, proportion lipidique et protéique), taux de respiration et d'excrétion de N et de P, de même que le ratio N:P de l'excréta.

L'objectif premier est d'explorer la base de données que nous avons nous-mêmes construite et d'examiner la distribution des valeurs de traits compilés entre les taxa et les habitats. Par le fait même, nous ferons également le point sur les traits pour lesquels il semble y avoir moins d'information disponible dans la littérature, que ce soit en milieu marin ou dulcicole. Nous décrirons ensuite les relations entre les traits par approche corrélationnelle et tenterons de déterminer la présence de patrons entre les unités taxonomiques du zooplancton crustacé (i.e. calanoïdes, cyclopoïdes, daphniidés et les autres cladocères), de même qu'entre les habitats principaux des espèces (environnement marin ou dulcicole). Nos hypothèses générales sont les suivantes :

1. les relations linéaires entre (a) la taille et la masse, (b) la masse et les taux métaboliques et (c) entre les taux d'excrétion de N et P seront les plus fortement corrélées;
2. les coefficients allométriques entre la masse et la longueur du corps seront de ±3 et varieront selon la différence entre les formes corporelles typiques des deux grands groupes de zooplancton : copépodes (calanoïdes, cyclopoïdes) versus cladocères (daphniidés et autres);
3. les coefficients de régression des taux métaboliques (respiration et excrétion) en fonction de la masse des organismes sera de ±¾ (ou de -¼ pour les taux exprimés par unité de masse);
4. compte tenu des ratios corporels N:P moyens connus chez les groupes de zooplancton, le ratio N:P observé dans l'excrétion sera limité en phosphore (>16) pour ce qui est des daphniidés (principalement retrouvés en eaux douces), mais limité en azote (<16) pour les copépodes (fortement dominants dans les systèmes marins) et les autres cladocères (essentiellement présents en eaux douces). De ce fait, nous anticipons que le ratio indiquera un apport limité en N en milieu marin, mais près de l'équilibre en milieu dulcicole.

Pour ce faire, nous caractériserons quantitativement les relations allométriques, entre les taux métaboliques et la masse corporelle, puis entre les taux métaboliques eux-mêmes afin de comparer les coefficients obtenus entre les groupes et habitats, puis à ceux rapportés dans la littérature. Les équations générales obtenues pourront ultimement être utilisées afin d'estimer la valeur de traits plus difficilement mesurables à partir de mesures plus facilement accessibles. L'usage de ces équations faciliterait entre autres l'incorporation de traits physiologiques dans la caractérisation de communauté reposant sur un assemblage ou une combinaison de traits.

L'objectif final de cette étude est d'établir un cadre de travail conceptuel afin de classifier les traits du zooplancton en vue de pouvoir mieux les lier aux processus écosystémiques qu'ils affectent. Notre catégorisation se base sur le budget énergétique des organismes, intégrant ainsi les traits physiologiques souvent omis dans les études, de même que sur les fonctions écosystémiques connues pour être influencées. Nous espérons que notre contribution assistera les écologistes dans le choix des traits utilisés pour décrire les communautés de zooplancton et stimulera l'intégration entre les champs de l'écologie des communautés et de la biogéochimie.

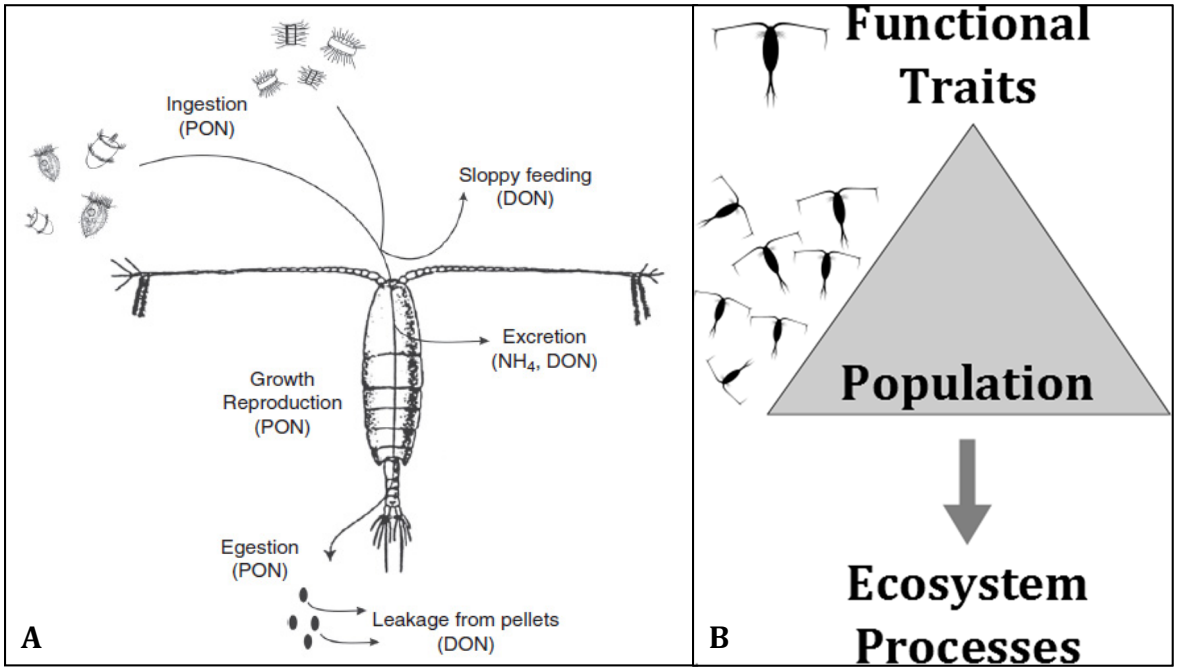

Figure I. A. Voies de consommation, transformation et libération d'azote par le zooplancton (PON : azote organique particulaire; DON : azote organique dissous) (modifié par Steinberg et Saba, 2008, originalement de Møller *et al.*, 2003). Tous ces processus au niveau de l'individu peuvent être quantifiés et rapportés en traits. **B.** Effet d'un trait présenté par plusieurs individus de la même espèce (i.e. rapporté à l'échelle de la population) sur les processus d'un écosystème. La nature de l'effet dépend du trait, la magnitude de l'effet dépend de la taille de la population qui partage le trait.

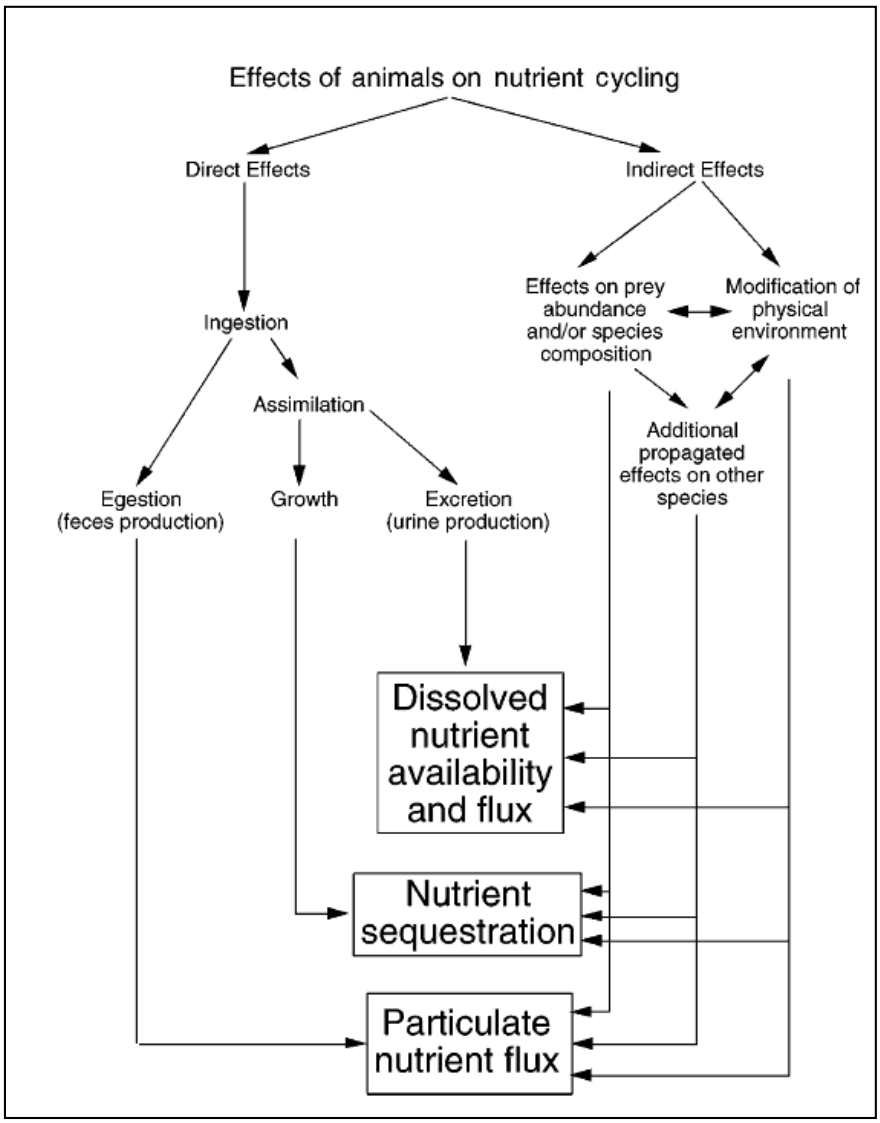

Figure II. Diagramme schématique incorporant les effets directs et indirects qu'ont les animaux sur le cycle des nutriments dans les écosystèmes aquatiques (tiré de Vanni, 2002).

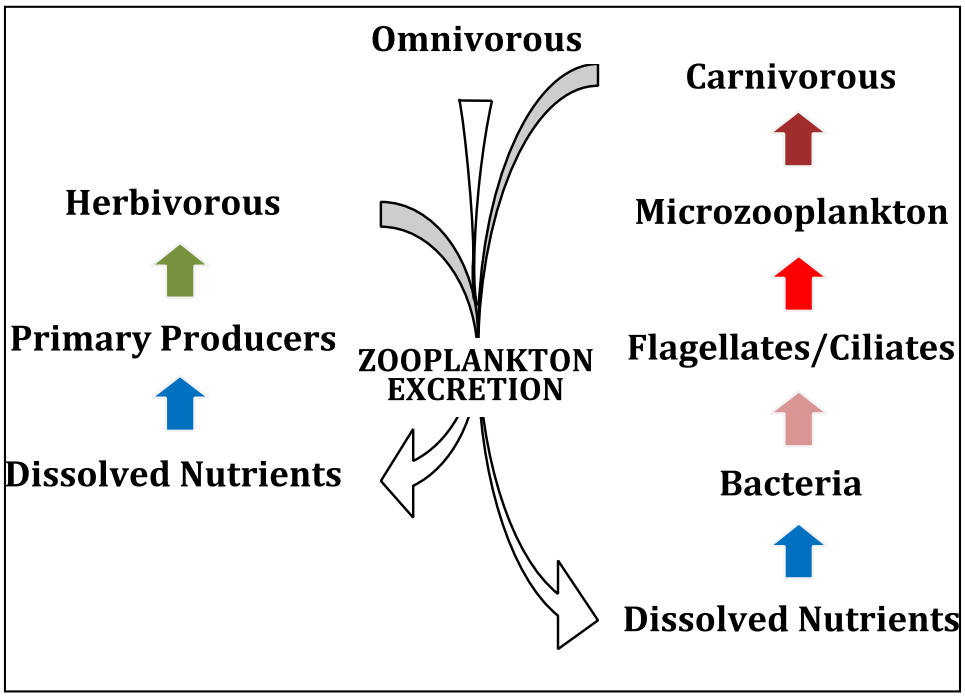

Figure III. Principe du recyclage des nutriments dissous par l'excrétion de zooplancton de différents groupes trophiques : herbivores, omnivores et carnivores. Les voies illustrées comprennent un aperçu des maillons classiques impliqués dans les microchaînes trophiques ayant comme maillon supérieur le zooplancton herbivore ou carnivore. L'énergie et les éléments remis en circulation via l'excrétion regagnent la chaîne alimentaire et traversent un nombre de maillon variable selon la position / groupe trophique du zooplancton.

Chapitre 2: *Zooplankton functional traits: Linking organisms to ecosystems*

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Article en préparation pour la revue *Ecology*

Abstract

The use of traits to characterize communities is proposed to be a more effective way to link community structure to ecosystem function. Organism morphology, corporal stoichiometry and physiology can be more readily linked to large-scale processes through functional traits, by providing information on interspecific and species-environment interactions. Given their key trophic position in aquatic ecosystems, zooplankton affect energy fluxes and element processing, making these organisms a good model for individual-ecosystem functioning linkages. Here, we compiled a large database of zooplankton species and their traits contributing directly or indirectly to C, N or P ecosystem fluxes. We identified gaps in the literature, explored cross-correlations among 16 traits, and examined the effects of taxonomy and main habitat (marine vs. freshwater) on these relationships. Specifically, we quantitatively described mass-length relationships, the scaling of respiration rates and N and P excretion rates with body mass, as well as the stoichiometry among these metabolic rates. Respiration and excretion rates followed mass-dependent scaling relationships in both major habitats, in line with the metabolic theory of ecology, although exponents were generally higher than predicted, ranging from 0.70 to 0.90. The strongest and most surprising effect that we found was the influence of habitat on zooplankton allometry and respiration; freshwater species had a lighter mass for an equivalent body length and three times higher mass-specific respiration rates as compared to oceanic species. These fundamental differences have potential implications for ecological strategies and overall carbon storage and fluxes between aquatic ecosystems. This synthesis is among the first to quantify multiple trait relationships and offer tools to link individual organisms to the ecosystem processes they influence. We

propose a new trait classification framework for zooplankton with the aim to promote a more complete integration of community ecology and aquatic biogeochemistry through the use of traits.

1. Introduction

One of the most classic paradigms in ecology is that organisms are fundamentally integrated in, affected by and affecting their physicochemical and biological environment (Elton, 1927; MacArthur, 1955; 1972). The activity of individual organisms, including their population dynamics and community interactions are known to influence ecosystem properties in both space and time via their behaviour, biomass changes and metabolism (Jones and Lawton, 1995; Rosenzweig, 1995; Chapin et *al*., 2000; Vanni, 2002; Pacala and Kinzig, 2002; Enquist *et al.*, 2003; Allen *et al*., 2005). Clearly characterizing how changes in community composition mechanistically alter ecosystem functions however remains a major challenge (Grime, 1998; Loreau *et al*., 2001; Hooper *et al*., 2005). One way to more fully assess how biological communities influence ecosystems is to classify the broader ecological roles of species within communities using a trait-based approach (Chapin *et al*., 1996; Lavorel and Garnier, 2002; Eviner and Chapin, 2003; Eviner, 2004). Functional traits denote individual-level characteristics of a organisms, such as morphological, physiological or behavioural features, that provide information on interactions within their food web and with their environment, including feedbacks that influence different ecosystem functions (Díaz and Cabido, 2001; Violle *et al*., 2007). As a result, a functional description of a community may be more relevant for predicting species-ecosystem relationships than other diversity metrics such as the number of taxonomic species

(Tilman *et al*., 1997; Bengtsson, 1997; Walker *et al*., 1999; Norberg *et al*., 2001; Hooper *et al*., 2005).

Although the effect of an individual trait in a single organism is likely to be negligible for ecosystem processing, this may no longer be the case when the trait effect is scaled to the population- or community-level. Ecosystem processes, such as energy and elemental fluxes, storage and turnover, are not only influenced by the overall biomass of a community but likely also by its structure (Vanni, 1988; Balseiro *et al*., 1997; Schindler *et al*., 1997; White *et al*., 2007; Enquist *et al*., 2009). Although the use of traits may best link organismal effects to their ecosystems, this approach is either rarely implemented (Hillebrand and Matthiessen, 2009), or when proposed, linkages are not always quantified. Furthermore, most trait-based studies tend to use traits that are more easily measurable or more commonly available, rather than focusing on traits that are best related to the ecosystem function of interest (Petchey and Gaston, 2006). To some extent this discrepancy depends on whether the utilization of traits is to reflect ecosystem process effects on communities, in which case "response traits" are measured (e.g. Woodward and Diament, 1991; Keddy, 1992; Lavorel *et al*., 1997; Barnett and Beisner 2007; Beisner and Longhi 2013). Our approach however focuses on the less commonly applied "effect traits", those traits by which individuals and community structure affects ecosystem-level processes (Calow, 1987; McIntyre *et al*., 1999; Díaz and Cabido, 2001; Lavorel and Garnier, 2002; Eviner and Chapin, 2003).

In aquatic environments, zooplankton occupy a central and pivotal position in food webs, making them key actors in trophic interactions and important mediators of energy and material fluxes in ecosystems (Lampert *et al*., 1986; Elser *et al*., 1988; Sterner, 2009).

Although several functional descriptions and trait classification schemes have recently gained popularity in zooplankton ecology (Barnett *et al*., 2007; Merico *et al*., 2009; Kiørboe, 2011; Litchman *et al*., 2013; Barton *et al*., 2013), most of these remain qualitative or conceptual and few have applied this approach to concretely link zooplankton community structure to ecosystem functions. We conducted a meta-analysis on crustacean zooplankton species traits contributing directly or indirectly to C, N and P fluxes in aquatic ecosystems using a large amount of trait information available in the literature. Our study includes data on traits related to body size, elemental and biochemical body composition, respiration and excretion rates and stoichiometric ratios. Although relationships for zooplankton metabolism or nutrient recycling as a function of body mass or elemental composition of organisms are known (Peters, 1983; Ikeda, 1985; Sterner, 1990; Sterner and Elser, 2002; Ikeda *et al*., 2001; Sereda and Hudson, 2011; Kiørboe and Hirst, 2014), few studies have examined the relationships amongst those traits from a functional diversity perspective, as well as their correlation structure.

Here, we synthesize and review a large number of observations on zooplankton traits likely to influence ecosystem processes and identify gaps in the literature to help direct future research efforts. We then explore the relationships between all traits and examine whether these relationships vary by major taxa or by habitat type (marine versus freshwater). More specifically, we quantitatively characterize and compare mass-length (allometric) relationships, the scaling of respiration rates and N and P excretion rates with body size, as well as the stoichiometric relationships among these metabolic rates. Finally, we provide a conceptual framework for categorizing zooplankton traits that integrates both organismal and ecosystem functions. The goal of this framework is to stimulate

ecologists to derive or develop more appropriate functional species groupings that may more readily link communities to various ecosystem processes of interest. Overall, this synthetic analysis provides new insights into the functional structure of zooplankton communities and increases our mechanistic understanding of the influence of zooplankton on aquatic ecosystems.

2. Methods

2.1 Database compilation

Web of Science and Google Scholar databases were searched in 2012 (January through November) to find articles on zooplankton nitrogen and phosphorous content and excretion rates. Two separate searches were conducted including the following keywords: (i) zooplankton* AND (nitrogen* OR ammonia* OR phosphorus* OR phosphate*) AND excretion*, (ii) zooplankton* AND (elemental* OR nitrogen* OR phosphorus* OR lipid* OR protein*) AND body* AND composition*. Both databases were revisited in 2013 (November to December) for information on zooplankton carbon content and respiration rates, using two combinations of search terms: (i) zooplankton* AND respiration*, (ii) zooplankton* AND (elemental* OR carbon*) AND body* AND composition*. We then manually searched through the title, abstract, results and, if necessary, the full text of each article to decide whether the study matched our selection criteria. References cited in these articles were also checked and considered in our literature search. We only selected studies that (i) included information for crustacean meso- and macrozooplankton, i.e. essentially copepods and cladocerans (ostracods or marine mysids, amphipods, euphausiids were not included), (ii) provided species' dry mass data from which we could

estimate individual-level excretion and respiration rates (or, inversely, estimate mass-specific rates), and body composition as % elemental proportions of unit dry mass. Note that most studies refer to body mass as body weight (mg); although this term has been pervasively used in literature, the term body mass will be used in this study. It should also be noted that the term zooplankton used throughout this text refers to the crustacean meso- and macrozooplankton taxa targeted in the present study.

For studies on zooplankton respiration, rate estimates based on ETS (electron transport system) activity were excluded in order to minimize variance across species for this trait caused by methodological differences. Although ETS is now considered as a good predictor of zooplankton respiration rates (Bode *et al*., 2013), a larger number of literature estimates are still available for more traditional approaches like measurements of oxygen metabolism. We included studies from a wide range of marine and freshwater environments, although most of the articles that we retained were from temperate regions. Ambient or experimental temperatures in each study of zooplankton metabolism (i.e. for respiration and excretion rates) were recorded in order to apply a standardized temperature correction. Data were often extracted directly from figures in articles or reference books using the software *Datathief III*, (version 1.6, Bas Tummers ©). Note that only articles from journals that were accessible through the Université de Montréal subscription to the Web of Science were used (1945 – present).

A database extended from Barnett *et al*. (2007), elaborated upon a working group sponsored by the Canadian Institute of Ecology and Evolution (CIEE) that contained body length and dry mass estimates for 144 crustacean zooplankton species, mostly found in freshwater habitats was also used. The original estimates of body size in this database

were enhanced by the inclusion of data from several North American datasets including the North Temperate Lakes Long Term Ecological Research (NTL-LTER) site in Wisconsin, U.S.A. and data from the Experimental Lakes Area (ELA), part of the Canadian Department of Fisheries and Oceans (DFO) until 2012. Dry mass estimates were based on taxon-specific length-mass allometric equations (McCauley 1984, Culver *et al*. 1985).

We are aware that more information on species body size is available in the literature, especially for marine species. However it should be noted that the focus of the study was initially on zooplankton excretion, with respect to the stoichiometry of body composition, but the interest of study evolved to consider a broader suite of available traits, including respiration, in order to make direct links to ecosystem function.

2.2 Data treatment

Species were first classified according to their main habitat type, i.e. freshwater or marine. The few brackish water species included in the dataset were grouped with marine species. To avoid pseudo-replication in further statistical analyses, all trait information on juvenile stages and male individuals were removed and only data on adult females (i.e. C6F for copepods) were considered for trait relationships.

Metabolic rates vary as a function of temperature. Therefore all respiration and excretion rates were standardized to 18°C according to the van't Hoff rule, commonly used to characterize the relationship between metabolic rates and temperature in zooplankton (Hernández-León and Ikeda, 2005):

$$Q_{10} = (k_1/k_2)^{10/(t_1-t_2)} \qquad \text{(Eq. 2.1)}$$

where k_1 and k_2 are the respiration rates corresponding to temperatures t_1 and t_2. We used Q_{10} approximations adapted for respiration, and N and P excretion in zooplankton. According to Ivlena (1980) and Ikeda *et al*. (2001), the Q_{10} for marine copepod respiration rates ranges from 1.8 to 2.1. Considering that no comparable compilation of respiration data exists for freshwater species, we followed Hernández-León and Ikeda (2005) suggestion and applied the relationship developed for marine zooplankton to freshwater taxa. Likewise, we used mean Q_{10} estimates for ammonia and phosphate excretion derived from marine species, which are 2.0 and 1.55, respectively (Bidigare, 1983, Ikeda, 1985, Ikeda *et al*. 2001, Regnault, 1986).

2.3 Meta-analysis limitations

Given some of the large information gaps and data heterogeneity in the literature, several limitations in the data available restricted the scope of the analysis and sometimes prevented us from using formal meta-analytical methods (Gurevitch and Hedges, 1999; Koricheva *et al*., 2013). Regardless of the limited number of observations for our empirical review, there was a lack of stoichiometric information on food supply that would have permitted us to include its effect on zooplankton excretion in our analyses. Instead, most studies only offered algal species, but not their composition. The non-homeostatic nature of phytoplankton made it impossible to estimate stoichiometric ratios despite the recognized relevance of this environmental driver.

Broadly speaking, literature meta-analysis such as ours presents recurring limitations. First, methods used to measure traits (such as body composition or metabolic rates) differ between studies, introducing potential sources of variation (i.e. noisy data).

Second, the number of observations (ranging from 1 to 72 individuals in our case) used to estimate a trait value for a given species differed. Furthermore, it was impossible to weight the estimates by the number of observations when variance was not reported, as recommended by Koricheva *et al.* (2013). Although these sources of variation sometimes limited our possibilities in terms of data analyses, we still explored all relationships among traits by giving equal weight to all trait values. However, a strength in our study is that we only considered raw data to develop relationships which is more rigorous than using data inferred from a statistical test (Valentine *et al*., 2010).

2.4 Statistical analyses

All analyses were conducted in R, version 2.14 (R development Core Team, 2011). Given that the number of measured individuals per trait varied among species, as did the number of traits per individual, we averaged all observed values for each trait per species, and used these means as observations in regressions. Dotcharts were used to visualize data and identify potential outliers; Dixon's Q test was used to decide whether or not these points were to be excluded (Dean and Dixon, 1951, Rorabacher, 1991). We only performed this test once for each variable and used 95% confidence intervals in order to apply conservative criteria when labelling data points as outliers (i.e. to reduce the likelihood of rejecting legitimate values containing no systematic error). Outliers were removed prior to statistical analyses, either because of possible measurement error, or simply because the species is known to have ecologically extremely different traits as compared to the majority of crustacean zooplankton (see Table A.I for the list of these species). An example of this is the freshwater cladoceran *Leptodora kindtii*, which is known to be considerably

larger than all other freshwater species reaching a body length as high as 15.8 mm. It should be noted that including or rejecting outliers led to the same patterns and statistically-significant results, although the *p* values of the relationships changed slightly.

Box-plots were used to compare trait values distribution among taxa and habitats. When a comparison was particularly of interest (e.g. for N:P ratios in body composition and excretion), we used traditional t-tests to determine if a taxonomic group was a significantly different from other taxa. All data were then ln-transformed prior to conducting further analyses to best approximate normality.

In order to explore relationships among species traits, we computed a correlation matrix of Pearson's correlation coefficients. Relationships between pairwise trait combinations were investigated in further analyses in order to detect differences among taxa and habitats. For several significant relationships, we tentatively developed predictive equations based on easily-measured traits. To evaluate how dry mass varies with body length, we used analysis of covariance (ANCOVA) to include "taxon" or "main habitat" as covariates, to uncover potential differences in length-mass relationships across taxonomic groups or habitats. We then calculated separate allometric equations using either all species in the database or only a subset of species from a given habitat (freshwater or marine) and/or by taxonomic group. To describe the allometric relationship between zooplankton body length and dry mass across species means, we used the well-established power law (Bird and Prairie, 1985):

$$\ln W = \ln (a) + b\ (\ln L) \qquad \text{(Eq. 2.2)}$$

where W is body mass and L corresponds to the body length of the species. To estimate allometric coefficients (i.e. the scaling exponent, or the slope term *b* in equation 2.2) of the

mass-length relationship among all species, taxa or main habitats, we computed model II simple linear regressions by major axis, using the library "lmodel2" (Legendre, 2013). Model II regressions were used because we could assume that the error variance of both variables was relatively similar and because we aimed to compare the slopes of the relationships between the same two variables measured under different conditions (Jolicoeur, 1990). The major axis method seemed like the most appropriate to estimate parameters of an equation that describes the functional relationship between two morphological attributes, namely body mass and length, because we cannot state which of the two traits is the dependent or independent variable considering that their influence is bidirectional (Legendre and Legendre, 2012).

To quantify relationships between respiration and excretion rates (in terms of N and P) versus body mass, we used simple linear regressions by ordinary least squares (OLS). The OLS method was sufficient in this case because we could reasonably assume that the error variance of the measured physiological rates was significantly higher than the one associated with body mass measurements and because it is well-known that mass influences metabolic rates, rendering obvious the determination of the dependent and independent variables. We regressed respiration and excretion rates against body dry mass using ln-transformed data. Confidence intervals were calculated based on the standard errors of the regression models. Where possible, we also conducted ANCOVAs with "habitat" or "taxon" as covariate in order to determine if patterns could be observed among taxonomic groups or habitats. As for relationships between physiological traits (i.e. excretion and respiration rates), we used model II simple linear regressions to quantitatively evaluate relationships between metabolic rates.

3. Results

3.1 Overview of meta-analysis

Our literature search yielded 8871 and 508 observations for marine and freshwater crustacean zooplankton traits respectively, corresponding to 134 marine and 153 freshwater species (outliers removed). Studies on marine zooplankton often reported information on the same commonly-studied species, whereas studies on freshwater zooplankton frequently described whole community assemblages with trait value averages reported for every species. This explains the discrepancy between the number of observations of a given trait versus the total number of species between habitats. Most studies reporting on crustacean zooplankton provided information on body size, making length and dry weight the most commonly available species traits from both habitats (Table 1). Marine species were significantly larger on average than freshwater ones. Indeed, the mean body length (BL) and dry mass (DM) were 2 and 7 times higher on average respectively, with a broader range of values in zooplankton from marine systems versus freshwaters.

Species-level values of elemental body composition (N, P and C content), biochemical composition (lipid and protein content) and physiological traits (respiration and nutrient excretion rates) were in all cases much more common for marine than for freshwater species (Table 1). Although the overall means and ranges for C and N content were similar between marine and freshwater zooplankton, we did observe some differences in P body content as well as the stoichiometry of the N:P body ratio among taxa, where P content and ratios were on average higher and lower, respectively, for freshwater species (Table 1). This was largely a function of freshwater daphniids, which

had significantly more P in their body composition, and thus lower N:P body ratios as compared to other cladocerans and copepods (Fig. 1a). Ratios were similar among freshwater and marine cladocerans and calanoids, but they diverged strikingly in cyclopoid species (Fig. 1a). However, the latter observation is based on one observation per habitat only and would need to be confirmed. The N:P ratios of excreted products were highly variable in both marine and freshwater species, varying by an order of magnitude (Table 1). Although the mean and range for this stoichiometric ratio was similar between marine and freshwater species, we did observed a difference among taxonomic groups (Fig. 1b). Daphniids had significantly higher N:P ratios in their excreted products than other cladocerans and copepods, (Fig. 1b), consistent with their body requirements (Fig 1a).

Biochemical composition data were mostly reported as either total mass of proteins, total mass of lipids or by type (i.e. lipid classes or amino acid composition), however we were only interested in the total body proportion (%). Of the limited number of freshwater studies found, most reported differences among stages (especially during diapause stage (C5) for copepods), and between sexes within a given species. Fewer than five species from freshwaters were compiled in our literature survey (i.e. 3 cladoceran and 2 copepod species), suggesting that information on proportional biochemical composition for freshwater zooplankton is a major knowledge gap. Note that information on males was excluded for interspecific trait comparisons, thus further reducing the total number of observations for our analysis. Despite the scarcity of data matching our selection criteria, values of total protein content were similar between freshwater and marine species.

However, we did find overall higher values of total lipid content in marine organisms (Table 1).

For physiological traits, ranges for individual respiration and N and P excretion rates varied over two to three orders of magnitude in marine zooplankton whereas for freshwater species, rates ranged from only one to two orders of magnitude (Table 1). Individual mean respiration and N and P excretion rates were on average approximately 3, 6 and 9 times higher in marine versus freshwater species. However, when expressed per unit dry body mass, freshwater species were approximately 3, 2.5 and 5.5 times higher for respiration, N and P excretion (Table 1).

3.2 Data analyses

In order to evaluate how traits covaried, we explored the correlation coefficients among all trait combinations (Table 2). The number of observations for each pairwise comparison differed greatly among relationships and is indicated in the upper panel of the correlation matrix. Certain traits, such as BL, DM and those related to physiological processes resulted in a large number of significant correlations. Relationships between these traits were explored further in subsequent analyses in order to characterize differences among taxa and habitats and in order to develop predictive relationships between more commonly available traits versus those with fewer observations.

3.2.1 Allometric relationships

Using reduced major axis in simple regression, we found a strong overall relationship between body length (BL) and dry mass (DM) across all crustacean

zooplankton species across habitats (corresponding to 98 copepods and 85 cladocerans in this study), with a R^2 of 0.8 (Table 3, Fig 2a). Although both habitats span a broad range in values, it is clear from the distribution of the data that marine species dominate in the upper quadrant. In order to determine, how DM varies with BL between major habitats and among taxa, we used an ANCOVA approach. All effects in both ANCOVA models were statistically-significant ($p < 0.0001$) (Figs 2b and c). Given that differences among taxa and between habitats appeared to influence both the slope and the intercept of the overall allometric relationship, separate length-mass linear regression equations for all possible combinations were performed (Table 3).

When the dataset was divided according to taxa but pooled across habitats, significant differences in the BL-DM relationships were observed among taxonomic groups (Fig. 2b), again with very high R^2 values ranging from 0.70 to 0.82 (Table 3). Calanoids gained more mass across a similar increase in body length than did all other taxa, with an allometric coefficient (i.e. scaling exponent, which corresponds to the slope of the ln-transformed equation) of 3.469 (Table 3). This scaling exponent was almost twice as large as the one observed for non-daphniid cladocerans at 1.907 (Table 3). The allometric coefficient for daphniids was 2.735, which was significantly higher than the one observed for other cladocerans, but was similar to the one observed for cyclopoids at 2.713 (Table 3).

When relationships were evaluated between habitats a significantly higher slope and intercept was observed for marine as compared to freshwater zooplankton (Fig. 2c). This difference in patterns not only supports that oceanic species are heavier for an equivalent length than species found in freshwaters, but that marine species gain more in

mass as they increase in length (Table 3). Again relationships were very strong and highly significant explaining a high proportion of the variance in both habitats. Given the differences and strong relationships we observed among taxa and between habitats, ANCOVAs were performed to explore patterns within taxa between marine and freshwater habitats. The general pattern that emerged in the relationship between habitats (Fig. 2c), wherein freshwater species had lighter mass compared to marine species for a given body length, was also observed when different taxa were considered independently (Table 3). Most obvious was the pattern between calanoids from different habitats, where the intercept of the relationship for marine species was almost four times higher than the one observed for freshwater species, whereas the allometric coefficients were relatively similar between the two equations (Table 3). The same pattern emerged with cyclopoids, although the number of observations for marine systems that fulfilled our selection criteria was rather limited (Table 3). Comparisons for cladorecans were not possible with this dataset as marine representatives were too rare. Interestingly the patterns observed within taxa suggest that lighter zooplankton relative to their length in freshwaters may not simply be a function of cladoceran species being more abundant in freshwaters, or a matter of shape variation across taxa, but that the differential allometry observed between marine and freshwater crustacean zooplankton may indeed be a habitat-related trait.

3.2.2 Patterns in trait combinations

Of the 16 traits evaluated in the correlation matrix (Table 2), the greatest number of significant correlations emerged with DM, which served as an excellent predictor

variable for many other traits, particularly physiological rate variables (Fig. 3). In accordance with allometric theory, individual N and P excretion rates were all significantly ($p < 0.0001$) and positively related to species DM (Figs 3a and b), explaining 73% (n=71) and 72% (n=47) of the variance respectively using the following models:

$$\ln(\text{N-NH}_4^+ \text{ excretion rate}) = 0.84 \ln(\text{DM}) + 2.50 \quad \text{(Eq. 3.1)}$$

$$\ln(\text{P-PO}_4^{3-} \text{ excretion rate}) = 0.70 \ln(\text{DM}) + 0.56 \quad \text{(Eq. 3.2)}$$

where rates are expressed in nmol (N or P) $\text{ind}^{-1}\ \text{h}^{-1}$ and DM in mg.

An ANCOVA did not reveal any significant difference in these relationships between habitats. Although observations from both environments fell clearly along the regression line, marine observations were however more clustered at the higher end of the graph (Figs 3a and b), again highlighting the greater overall individual excretion rates of both N and P from the typically larger marine zooplankton (Figs 3a and b). No significant difference was observed among taxonomic groups either. This however may have been due to a limited number of observations for most species groups with the exception of marine calanoids. Copepods tended to excrete more P than cladocerans (represented primarily by daphniids) in freshwaters, for the same body mass (Fig. 3b). This pattern supports as the stoichiometric needs of daphniids compared to copepods (Figs 1a and b).

Interestingly, the relationship between DM and individual respiration rates was different between marine and freshwater zooplankton (Fig. 3c). An ANCOVA revealed that although the scaling exponent of this relationship was not significantly different between systems, a significant difference between intercepts was observed. Indeed, respiration rates were on average three times higher for a given mass of a freshwater zooplankton compared to marine species, based on the following equations:

$$\ln(\text{respiration rate})_{\mathbf{FR}} = 0.82 \ln(\text{DM}) + 1.24 \quad \text{(Eq. 3.3)}$$

$$\ln(\text{respiration rate})_{\mathbf{MA}} = 0.90 \ln(\text{DM}) + 0.21 \quad \text{(Eq. 3.4)}$$

where respiration rate is expressed in μL O_2 ind^{-1} h^{-1} and DM in mg. DM explained considerably more variance in individual respiration rates in freshwater zooplankton than in marine species at 94% (n = 17, $p < 0.0001$) and 54% (n = 42, $p < 0.0001$) respectively.

Physiological rates measurements were in all cases significantly and negatively related to body mass when expressed per unit DM, with the exception of mass-specific respiration in marine zooplankton where the relationship was not significant (Fig. 3f). These relationships were comparatively weaker with only 12% of variance explained for N and 41% for P specific excretion rates. However these trends did support that smaller organisms, mostly freshwater species, tended to have a more rapid mass-specific metabolism, regardless of their taxonomic group (Figs 3d-f). As for mass-specific respiration, DM explained 41% of the variance in freshwater respiration rates, whereas the relationship for marine respiration rates was not significant.

All significant trait relationships in the correlation matrix (see Table 2 for *r* values) yielded significant regression results ($p < 0.05$). However, in the case of the relationships referring to elemental and biochemical composition of zooplankton, those that predicted other traits from body N or P content were typically much stronger than any other body composition trait. The strongest relationships were largely intuitive with body N and P content being positively and negatively related to N:P body ratios, respectively (Table 2).

Only four relationships between elemental body composition traits and excretion rates and ratios were statistically significant: N excretion rates versus N content and P

content, and P excretion rates versus P content and N:P body ratio (Table 2). However, these relationships were weaker (see Fig. A.II for more details).

Physiological traits were for the most part strongly correlated (Table 2). Model II simple regressions were used to quantitatively characterize the significant relationships between metabolic rates. Individual P and N excretion rates were highly related ($R^2 = 0.84$, n = 42, $p < 0.001$) (Fig. 4a), according to the following equation:

$$\ln(\text{P-PO}_4^{3-}\text{ excretion rate}) = 0.95 \ln(\text{N-NH}_4^{+}\text{ excretion rate}) - 1.97 \quad \text{(Eq. 3.5)}$$

where excretion rates are expressed in nmol (N or P) $\text{ind}^{-1}\ \text{h}^{-1}$. No significant differences between habitats or taxa were observed in this relationship. Interestingly, the stoichiometry of this relationship indicates an average molar N:P ratio of approximately 8 in zooplankton excretion, thus suggesting a recycled input generally limited in N. However, most species included in this relationship are marine copepods (76%) potentially resulting in a bias given the stoichiometry of their body requirements (Fig. 4a; Table 1).

Interestingly, a model II regression showed that N excretion rates were strongly and positively related to respiration rates ($R^2 = 0.74$, n=37, $p < 0.001$) (Fig. 4b):

$$\ln(\text{N-NH}_4^{+}\text{ excretion rate}) = 0.93 \ln(\text{respiration rate}) + 1.93 \quad \text{(Eq. 3.6)}$$

where excretion is expressed in nmol N- NH_4^+ $\text{ind}^{-1}\ \text{h}^{-1}$ and respiration, in µL O_2 $\text{ind}^{-1}\ \text{h}^{-1}$. This model indicated that for each µL O_2 respired, almost 6 nmol of N- NH_4^+ was excreted. Interestingly no significant relationship was observed between P excretion and respiration rates (Fig. 4c), albeit sample size was small. Limited data did not allow for further comparisons of traits among the taxon and habitat covariates of these relationships.

4. Discussion

Zooplankton play a pivotal role in aquatic ecosystems and although there has been a considerable amount of effort in promoting a trait-based approach for their characterization (Barnett *et al.*, 2007; Litchman *et al.*, 2013; Barton *et al.*, 2013), these studies typically remain mainly qualitative and descriptive. The novel aspect of our work was to put different traits into a quantitative context and characterize the relationships among several trait combinations, between habitats and among taxonomic groups. Although some of the relationships are known from previous studies (Peters, 1983; Ikeda, 1985; Sterner, 1990; Ikeda *et al.*, 2001; Sereda and Hudson, 2011; Kiørboe and Hirst, 2014), their applicability from a trait perspective has yet to be evaluated, as does the correlation structure among multiple traits. The results of our meta-analysis revealed fundamental differences among freshwater and marine zooplankton, even within a taxonomic unit, and provide mass-scaled exponents of metabolic rates. We believe that physiological traits may be the most useful ones to extrapolate the effect of organisms to an ecosystem context (Calow, 1987; Díaz and Cabido, 2001; Lavorel and Garnier, 2002; Alcaraz *et al.*, 2010). Finally, we propose a modified and more complete framework of zooplankton traits together with the ecosystem functions these traits are likely to influence.

4.1 Cross comparisons of trait variables

4.1.1 Data availability in the literature and knowledge gaps

In our review of published data on a diversity of crustacean zooplankton traits contributing to C, N or P fluxes, we examined both marine and freshwater species. Trait information for marine species dominated the literature (Table 1), an observation also

made by other large-scale studies on zooplankton metabolism (Wen and Peters, 1994; Hernández-León and Ikeda, 2005). Comparatively to studies on marine zooplankton, freshwater species appeared to be relatively less characterized in terms of elemental and biochemical body composition as well as metabolic rates (Table 1). This bias likely reflects a difference in research interests between limnologists and oceanographers where freshwater scientists likely focus more on community and population dynamics than marine scientists who are often concerned with zooplankton physiology. Irrespective of habitat type, there were also some traits for which information was generally scarcer, such as total biochemical body composition (Table 1). The aforementioned general knowledge gaps limit the scope of empirical model development, such as ours, that attempt to compare taxa and ecosystem types. Nevertheless, we were able to derive mean values of all traits among taxa and between habitats and robustly quantify several relationships.

4.1.2 Mean trait values

Many differences in mean traits were observed between marine and freshwater zooplankton and among taxonomic groups (Table 1, Figs 1 and A.I). Between habitats, marine zooplankton tended to have larger body size and expressed higher individual rates for nutrient excretion and respiration. Smaller freshwater zooplankton conversely had higher mass-specific physiological trait rates on average, reflecting allometric constraints on metabolism (Peters, 1983). Organismal metabolism is a fundamental process underlying individual- and population-level variables, and thus provides a clear mechanism for linking species traits with large-scale processes. Therefore, the observed difference between

freshwater and marine species metabolism clearly has implications for zooplankton-ecosystem processes linkages.

N:P ratios have been an important focus of ecological stoichiometric theory (EST) in zooplankton (Sterner and Elser, 2002). In our analysis, mean values of N:P body ratios were almost two-fold higher in marine species. This difference is consistent with the fact that cladocerans (especially daphniids) are known to have lower N:P body ratios than do copepods and the fact that cladocerans are considerably more abundant in freshwaters while copepods dominate in oceans (Andersen and Hessen, 1991; Elser and Hassett, 1994; Elser and Urabe, 1999). Furthermore, averaged trait values per taxon and habitat showed that species groups with higher N: P body ratios had lower N: P excretion ratios (Figs 1a and b), consistently with EST (Sterner, 1990; Hessen and Andersen, 1992; Sterner *et al.*, 1992). Our analyses revealed N: P ratios generally below Redfield's ratio (Redfield, 1958) in zooplankton excretion in all species groups, with the exception of daphniids (Fig. 1b).

Although this well-established stoichiometric concept could easily be seen in our dataset using box-plots, results were less apparent in broader cross comparisons using a regression approach. Indeed, certain relationships between elemental body composition and excretion rates and stoichiometric ratios were not significant, in contrast to those predicted by EST. This discrepancy could be a function of our inability to correct for large site variation in phytoplankton N:P ratio. According to mass-balance principles, the N:P ratio of animal excreta is a function of the imbalance between the nutrient ratios of the animal's body and the food it ingests. Given that phytoplankton are highly spatially variable in N:P content (Klausmeier and Litchman, 2004), due to their non-homeostasic nature (Sterner and Elser, 2002), it is possible that we did not detect the expected patterns in our

regression analysis because the effect of zooplankton body composition on excretion ratios could have been masked by site variability in food N:P ratio. Indeed, Elser and Urabe (1999) suggested that the N: P ratio of food may be more important in predicting excretion ratios than is zooplankton N: P body requirements. Alternatively, we might have not detected a relationship between body composition and excretion ratios because our species did not exhibit sufficient variance in P content. Indeed, organisms without bones such as zooplankton have lower corporal P variation, making their N:P body ratio less variable than vertebrates (Vanni, 2002; Vanni *et al*., 2002).

4.1.3 Allometry

The description of mass-length relationships across many species provides useful insights for broader patterns in allometric relationships than do those determined at the species-level (e.g. Cohen and Lough, 1981; McCauley, 1984; Culver *et al*., 1985; Ara, 2001). The scaling exponent of the overall mass-length relationship for crustacean zooplankton in our dataset was approximately 3 (2.8), corresponding to reported values in freshwater and marine large- and small-scale studies (McCauley, 1984; Omori and Ikeda, 1984). The observed differences in scaling exponents and intercepts of the linearized mass-length relationships across the major taxonomic units used in our analyses (e.g. daphniids, other cladocerans, cyclopoids and calanoids) appear to reflect body shape variation among groups (Martin, 1992). The similar relationships between daphniids and cyclopoids observed may result from a generally wider prosome in cyclopoids, as compared to calanoids of the same length, as well as slightly more elongated daphniids relative to most other cladocerans (Amoros, 1984). Of all taxa-specific relationships, non-daphniid

cladocerans had the lowest slope and highest intercept, indicating a higher body mass to equivalent length which might arise from their generally smaller and rounder body shape in other groups. Substantially higher intercept values were also found for some species-level relationships, such as congeners of *Holopedium*, *Bosmina* or *Chydorus* (McCauley, 1984).

In addition to the variation among species, zooplankton mass-length relationships are also known to vary seasonally, according to geographic location, due to fluctuations in temperature and food availability, and thus the physiological state of the animals (Ikeda 1974; Durbin & Durbin 1978; Viitasalo *et al*. 1995). Despite this great site-to-site variability, we surprisingly found a strong emergent difference in mass-length relationships between major habitats: marine species not only had a heavier body mass over freshwater species of equivalent lengths, but also had a greater increase in body mass for an increase in body length. These differences in allometry between habitats has, to our knowledge, never been noted before; likely because only very few studies compare data across aquatic ecosystems. Considering that the trend was observed both among and within our taxonomic groupings (Table 3), variation in the general body shape of dominant taxa (copepods in marine; cladocerans in freshwaters) cannot explain this difference. A possible explanation for greater body mass in marine environments would be a matter of buoyancy control. Given that many zooplankton species perform diel vertical migration, having a greater mass for the same length would help to counter their positive buoyancy in dense salt water. Potential density compensation by other tissues for marine copepods with wax esters (primary storage lipid in marine zooplankton) has already been discussed with in this context (Ackman, 1989). Since wax esters are of low

density, a zooplankter may control its buoyancy with greater mass in other tissues as compared to zooplankton using other lipid types (Ackman, 1989; Brett *et al*., 2009). Although our dataset does indicate that several marine species may have higher proportions of lipids in their body (Table 1), we could not evaluate the potential effect biochemical composition on their body mass variation. However analogous adaptations have been found for fishes (e.g. darters), where the length of swim bladders (internal gas-filled organ for buoyancy control) appear to not only be related to fish body size, but also to the type of habitat and swimming behaviour (e.g. midwater versus benthic) (Evans and Page, 2003). Generally, marine fishes have relatively smaller swim bladders than do freshwater species, to counter positive buoyancy in salt water (Evans and Page, 2003). To our knowledge, no study has formally compared freshwater and marine zooplankton body tissues in terms of their density; however, intra-habitat data on gelatinous marine zooplankton suggests that length-standardized dry mass correlates positively with salinity, suggesting local hydration in buoyancy control (reviewed by Hirst and Lucas, 1998). Although this relationship between salinity and mass is only known for certain species (Lucas *et al*., 2011), these results imply that body dry mass may be significantly overestimated in some gelatinous forms due to environmental salts concentrated in dried tissues. Whether a similar pattern holds for crustacean zooplankton warrants exploration. Nevertheless, the allometric difference we observed between marine and freshwater crustacean zooplankton suggests that mass-length relationships may not only be phylogenetic-constrained, but perhaps more importantly habitat-related.

4.1.4 Ecological implications of relationships among physiological traits

It is now well-known in biology that virtually all metabolic processes scale with body mass to the 0.75 power, or -0.25 on a mass-specific basis (Kleiber, 1961; Peters, 1983; West *et al*., 1997; Gillooly *et al*., 2001; Brown *et al*., 2004; West and Brown, 2005). The metabolic theory of ecology (MTE), which rationalized this energetic invariance concept with respect to ambient temperature (a parameter that was standardized in our study), is particularly relevant when assessing ecological implications of organismal physiological traits. Equations 3.1 to 3.4 quantify crustacean zooplankton excretion and respiration rates, as well as the stoichiometry according to the mass dependency of those processes. A clear pattern emerged from our dataset, despite all the noise related to site and species variation: respiration and excretion rates followed mass-dependent scaling relationships in both major habitats, faithful to MTE. While the scaling for P excretion versus body mass was slightly under 0.75 (0.70), N excretion as well as freshwater and marine respiration mass-relationships were above the 0.75 scaling law predictions (values of 0.84, 0.82 and 0.90 respectively). These slopes are within the range of values found in other zooplankton data compilations (Wen and Peters, 1994; Ikeda *et al*., 2001). They, however, indicated a differential response in respiration, and P and N excretion as body mass increases across zooplankton species, where N excretion increases at a faster rate than P excretion and marine respiration at a faster rate than freshwater respiration. This may have important implications when considering the size class of the community structure in aquatic food webs, where zooplankton communities predominated by larger species may potentially have a stronger influence on ecosystem element fluxes, not only in amount but also in the relative ratio of what is recycled. Although deviations from 0.75

may partly be due to noise in the data (perhaps especially for the relationship between mass and respiration with an R^2 of only 0.54), scaling patterns are known to differ across species according to both the spectrum of body sizes considered in an analysis and phylogenetic history (i.e. which species included) (Frost, 1980; Glazier, 2005; 2006; Kiørboe and Hirst, 2014).

Although the limited number of observations for certain taxa prevented us from detecting significant differences in excretion among taxa or habitat, the trends drawn from our regression analysis suggested that marine copepods, freshwater copepods and cladocerans may have similar scaling for excretion, but potentially different intercept values (Figs 3a, b, d and e). The fact that freshwater copepods and cladocerans seemed to qualitatively differ in their excretion rates is in line with previous work on zooplankton stoichiometry and EST, according to their body requirements. However, only patterns for P excretion, where daphniids were found to recycle less P in contrast to copepods, were coherent with predictions from EST (Sterner and Elser, 2002). This aspect has considerable implications for ecosystem nutrient cycling; indeed, seasonal or inter-annual increases in *Daphnia* abundance have already been associated with severe P limitation of phytoplankton in freshwaters (Elser *et al*., 1988; Urabe *et al*., 1995) When comparing excretion between freshwater and marine copepods in relation to the general regression line derived from both habitats, freshwater representatives appeared to have higher excretion rates for equivalent body mass, which would require more information to further confirm a habitat-related pattern (Figs 3a, b, d and e).

Regardless of taxonomic groups, individual and mass-specific respiration relationships showed a three-fold variation in intercepts between habitats, suggesting

substantially higher oxygen consumption by crustacean zooplankton biomass in freshwaters as compared to marine ecosystems (Figs 3c and f). Although literature data is limited for freshwater zooplankton respiration, this pattern has not yet been observed to our knowledge. While there is no comprehensive compilation of respiration rates for freshwater zooplankton comparable to those on marine species, Hernández-León and Ikeda (2005) tentatively made a comparison between habitats by predicting respiration rates in freshwater zooplankton across a suite of taxa (from rotatorians to dipterans) according to their mass, based on Ikeda's (1985) empirical model for epipelagic marine zooplankton. As they could predict reasonably well respiration values for freshwater species using an equation derived from marine species, they concluded that zooplankton respiration did not differ consistently across habitats. However, when only looking at crustacean zooplankton species that Hernández-León and Ikeda included in their analysis (Fig. 5.1 from Respiration in Aquatic Ecosystems, 2005), every single species of this group had respiration values underestimated by the relationship based on marine species. This suggests that a differential response in respiration may occur in freshwater crustacean zooplankton, particularly when compared to marine copepods.

Although the difference in respiration rates observed requires additional confirmation, we hypothesize that these differences may be related to the ecological strategies of the various groups. Zooplankton that relatively rapidly convert ingested resources into reproduction and growth, without food limitation, may express higher basal metabolic rates (Kleiber, 1961; Threlkeld, 1976; Grover, 1997). Consequently, higher respiration rates for freshwater species could reflect habitat-specific adaptations resulting from constraints imposed by the duration of the growing season and temporal

stability of freshwater environments (most freshwater species included in this studies came from temperate regions and therefore from sites that exhibit strong seasonality) (Sommer, 1989). In contrast, food supply may perhaps be scarce but more stable across seasons in marine environments (Legendre and Rassoulzadegan, 1995), which may favour energy storage by marine zooplankton (Grover, 1997). Differential investment in growth and reproduction, rather than long-term energy savings, could account for these differences in respiration rates between habitats. For example, embryo-carrying fishes with actively developing tissues (embryonic development) have higher mass-specific oxygen requirements than maternal tissues and may increase specific routine oxygen requirements for live-bearing females (Thibault and Schultz, 1978; Boehlert *et al*., 1991; Dygert and Gunderson 1991). Although several studies have characterized zooplankton physiological responses under variable environmental conditions (Threlkeld, 1976; Ikeda, 1977; Kirk *et al*., 1999, Alcaraz *et al*., 2014), the hypothesis that freshwater zooplankton may have higher mass-specific respiration rates due to different life history strategies deserves to be tested. Nevertheless, difference in basal metabolic rates according to aquatic habitats could also result in higher energy/prey consumption by freshwater zooplankton, which could influence other traits such as grazing and clearance rates, for example.

Correlations among physiological traits were amongst the strongest that we found (Table 2; Fig. 4), with N excretion rates related to both P excretion and respiration. This was expected because oxygen consumption is an indicator of total metabolism, which is strongly related to partial metabolic processes such as N and P excretion (Ikeda *et al*., 2001). The scaling exponent between P and N excretion was nearly 1 (eq. 3.5), similar to

that found by Wen and Peters (1994). Our model revealed a N: P molar ratio of 8 between N and P excretion, indicating a general input limited in N from crustacean zooplankton across aquatic environments (as observed in Fig. 1b); likewise, Sereda and Hudson (2011) suggested in their large-scale study an overall N:P ratio in zooplankton excretion ranging from 6.4 to 9.9. Although this relationship is mostly based on copepod data, it does reflect reality across aquatic environments and presents ecological implication for N-limited food supply for primary producers, especially for marine ecosystems which are known to be N-limited (Sterner and Elser, 2002). As for the relationship between N excretion and respiration (eq. 3.6), the slope was also very close to 1, again consistent with Wen and Peters (1994). This overall equation suggests a general N:O ratio for crustacean zooplankton, with 6 nmol of N- NH_4^+ excreted for each µL of O_2 respired. Molar N: O ratios may also provide information on the diet of zooplankton (Ikeda, 1977), and are specifically used to identify the type of metabolic substrate of catabolism, i.e. protein or lipid (Ikeda, 1974). Although this relationship can surely offer comparative coefficients, the mean N:O ratio provided here is not molar because of the difficulty in unit conversion (i.e. mol versus litre) when many environmental parameters are not available in studies (e.g. atmospheric pressure). Furthermore, fluctuations in both N:P and N:O ratios may be of particular of interest when assessing differential influence of temperature on physiological parameters.

4.2 Linking individuals to ecosystem processes

Our goal was to develop tools to better assess linkages between zooplankton communities and aquatic ecosystem processes. A trait-based approach conceptually represents a way to link all levels of ecological organization, from individuals to ecosystems,

but often trait descriptions fail to provide trait relationships in a quantitative way (Barnett *et al*., 2007; Litchman *et al.,* 2013), and to clearly afford direct links with ecosystem processes (Merico *et al*., 2009; Kiørboe, 2011; Barton *et al*., 2013). Here we compiled and analyzed a large database of trait information on crustacean zooplankton from a wide variety of literature sources, spanning various taxa from both marine and freshwater habitats to offer predictive equations and correlation coefficients among species traits. Other traits and species could be included to this database as they become available in the future, but the intention is that this current version promotes the use of a trait-based approach to explore general patterns across ecosystems as well as trade-offs among species traits. Although characterizing community structure through functional traits provides information on species and species-environment interactions (Díaz and Cabido, 2001), a general trait classification framework that concretely links organismal functions to ecosystem processes through species traits is still required.

The key traits of an organism are those that best characterize its fitness (Arnold, 1983; Geber et Griffen 2003; Reich *et al*. 2003). Fitness is a function of survival and reproduction, depending, in turn, on the fundamental activities and needs of a living organism, which are largely encompassed in a typical energy budget. At steady state, a balance is maintained between energy consumption and loss through daily active and basal metabolism, excretion (and egestion), growth and investment in reproduction (Kleiber, 1961; Kitchell *et al*., 1974; 1977; Kiørboe *et al*., 1985; Manyin, 2008). Additional energy must also be invested in anti-predator strategies to ensure survival (Visser, 2007; Kiørboe and Jiang, 2013). These activities and needs (hereafter referred to as organismal functions) rely on the details of the biology of an individual and may differ among organisms.

Zooplankton traits, whether they are regarded as morphological, phenological, physiological or behavioural features, represent a way to express these organismal functions. While such traits have evolved to meet the basic needs of an individual, optimizing its fitness, these traits also exert a strong impact beyond the organism itself; once scaled to population or community levels, they affect the stocks and fluxes of energy and the material at the ecosystem scale (Frangoulis *et al*., 2005; Alcaraz *et al*., 2010).

We propose a new, combined classification scheme that represents the different organismal functions through species traits along with the ecosystem functions that they directly influence (Fig. 5a). Traits are categorized according to the individual function(s) to which they pertain: energy consumption, active and basal metabolism, somatic growth and reproduction, predator avoidance, energy waste and loss. Some traits may also relate to more than one organismal function (e.g. body size) (Fig. 5a). Most traits listed, particularly those transcending more than one organismal function, may influence, or covary with, other traits (Table 2). Furthermore, how energetic loss or gain is divided among organismal functions can differ with life strategies or environmental conditions, potentially resulting in a trade-off between traits (Kiørboe *et al*., 1985; Bâmstedt, 1988; Grover, 1997; Kiørboe, 2011; Ji *et al*., 2012), that when scaled to the community level may have cascading repercussions on ecosystem processes.

In addition, most ecosystem functions may be affected by more than one zooplankton trait (Fig. 5a). These traits may come from the same or different categories, and can also influence the same ecosystem process differentially. For example, through feeding, zooplankton exert top-down control on algal biomass, affecting phytoplankton community composition and standing stock; conversely, zooplankton also sustain the

growth of phytoplankton via their excretion, thus enhancing primary productivity (Miller and Landry, 1984; Lehman and Sandgren, 1985; Vanni and Temte, 1990). Alternatively, a single trait may also influence more than one process. Continuing the preceding example, zooplankton release dissolved inorganic nutrients supporting primary productivity, as well as dissolved organic matter, which can sustain heterotrophic bacterial growth (Jumars *et al*., 1989; Carlson, 2002). All ecosystem processes affected by zooplankton ultimately contribute to larger biogeochemical cycles (Fig. 5a), either directly or indirectly; their effect however may differ among aquatic systems. For instance, through the cross comparison of traits of our meta-analysis, we found that some zooplankton traits values differ between marine and freshwater habitats. The difference in mass-specific respiration rates between habitats suggests a relatively higher oxygen consumption, and consequently carbon consumption, by zooplankton in freshwaters as compared to marine environments, with potential cascading repercussions on primary production.

Besides excretion, sloppy feeding or fecal pellet production are also known to contribute to biogeochemical cycles, especially in terms of organic matter fluxes (Fig. 5a) (Møller and Nielsen 2001; Wexels Riser *et al*., 2008; Tamelander *et al*., 2012). Physiological traits, in turn, depend on other characteristics, such as body size, corporal composition, or preferred diet, which contribute directly to the energy and material (i.e. stocks) in an ecosystem and thereby indirectly influence elemental fluxes in that ecosystem. These links with stocks and fluxes can be illustrated by considering the interactions of a typical zooplankter with its environment, in terms of energy transfers and chemical exchanges (Fig. 5b). Organismal functions regulating these transfers and exchanges are related to the respective ecosystem functions that they influence. This highlights the fact that all

organismal functions contribute to the individual objective of "Growth and Reproduction", influencing zooplankton biomass directly, and modulating biogeochemical cycles indirectly.

The framework presented here provides a unique hierarchical organization that identifies organismal needs or functions to species traits and links those traits to particular ecosystem functions using crustacean zooplankton as a model. Trait-based frameworks are often descriptive, focusing on multiple traits related to individual performance and trophic interactions. While life-history, "demographic" and "response" traits reflect individual, population- and community- levels of organization respectively, only the "effect" traits, such as physiological traits, can allow direct extrapolations to ecosystems processes (Calow, 1987; McIntyre *et al*., 1999; Lavorel and Garnier, 2002; Violle *et al*., 2007). Furthermore, quantifying multiple "effect" traits and evaluating how they covary with each other, among representative groups and systems, has yet to be done for many groups of organisms. The example here of how crustacean zooplankton traits fit into this hierarchical approach and how certain traits represent either a unique link to specific, or transcend multiple, ecosystem process(es) should serve as a guide to facilitate the integration of community ecology with biogeochemistry to improve our understanding of the biotic mechanisms controlling ecosystem functioning.

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LIST OF TABLES

Table 1. Number of individual observations (*N)*, number of species and summary of ranges and means of twelve quantitative functional traits in various crustacean zooplankton species included in the present analysis. Trait information is regrouped according to major habitat types. Data are for adult and females only. Species considered as outliers were removed from all species ranges and means. All respiration and excretion rates are standardized for temperature and are expressed both per unit dry mass and per individual. (See Tables A.I and A.II for the lists of species outliers removed and for species included in the present study; Fig. A.I for trait values distribution among habitats and taxa).

Abbreviations and corresponding units: Body Length (mm), Dry Mass (mg), N:P body ratio (molar), C ct (Carbon body content, %), N ct (Nitrogen body content, %), P ct (P body content, %), Prot ct (protein content, %), Lipid Ct (lipid content, %), Respiration rate (Temperature corrected–respiration rate, µl O2 $ind.^{-1}$ h^{-1} and µl O2 mg DM^{-1} h^{-1}), Ammonia excretion (Temperature corrected–ammonia excretion rate, nmol N $ind.^{-1}$ h^{-1} and nmol N mg DM^{-1} h^{-1}), Phosphate excretion (Temperature corrected–phosphate excretion rate, nmol P $ind.^{-1}$ h^{-1} and nmol N mg DM^{-1} h^{-1}), N:P excr. ratio (N:P excretion ratio, molar).

	Body Length	Dry Mass	N:P Body Ratio	C Ct (%)	N Ct (%)	P Ct (%)	Prot. Ct (%)	Lipid Ct (%)	Respiration Rate	Ammonia Excretion Rate	Phosphate Excretion Rate	N:P Excretion ratio
Marine Species												
N	287	1099	816	937	986	863	30	44	854	1024	972	959
Number of species	40	111	50	46	106	48	21	16	42	63	34	38
Range of species' means (per ind.)	0.47 – 4.88	0.002 – 4.02	16.5 – 48.4	39.4 – 49.7	6.14 – 13.1	0.58 – 1.56	27.7 – 73.3	5.20 – 59.7	0.0028 – 2.6096	0.0308 – 37.065	0.0266 – 7.2391	2.27 – 19.0
Range of species' means (per unit DM)	-	-	-	-	-	-	-	-	0.0148 – 8.1680	2.0455 – 60.18	0.4590 – 14.983	-
All species mean (per ind.)	2.16	0.72	31.0	42.9	10.1	0.79	49.7	25.6	0.4584	7.1880	1.4699	9.07
All species mean (per unit DM)	-	-	-	-	-	-	-	-	2.8190	18.836	3.2713	-

Freshwater Species												
N	173	174	23	<5	23	26	8	10	23	14	18	14
Number of species	147	152	19	<5	17	20	<5	<5	17	9	13	10
Range of species' means (per ind.)	0.200 – 3.8	0.001 – 0.23	7.85 – 53.9	47.0 – 48.0	8.2 – 12.4	0.41 – 1.14	48.7 – 70.0	9.90 – 23.5	0.0120 – 0.7650	0.0110 – 4.3500	0.0042 – 0.7740	3.02 – 25
Range of species' means (per unit DM)	-	-	-	-	-	-	-	-	3.3849 – 11.913	9.2110 – 127.86	0.9906 – 48.352	-
All species mean (per ind.)	0.97	0.01	18.9	47	9.48	1.14	56.2	16.7	0.1718	1.2127	0.1698	11.4
All species mean (per unit DM)	-	-	-	-	-	-	-	-	7.8690	46.806	18.364	-

Table 2. Matrix of correlation of selected crustacean zooplankton quantitative traits (all ln-transformed). All correlation coefficients are reported below the diagonal; significant ($p<0.05$) correlation coefficients are in bold. The number of species (*N*) for each pairwise correlation is indicated in parentheses, above the matrix diagonal.

Abbreviations and corresponding units: BL (body length, mm), DM (dry mass, mg), C ct (C body content, %), N ct (N body content, %), P ct (P body content, %), N:P body (N:P body ratio, molar), Prot ct (protein content, %), Lipid Ct (lipid content, %), Resp. rt. (ind.) (Temperature corrected–respiration rate, µl O2 *ind.*$^{-1}$ h^{-1}), Resp. rt. (DM) (Temperature corrected–respiration rate, µl O2 mg *DM*$^{-1}$ h^{-1}), NH4+ ex. rt. (ind.) (Temperature corrected–ammonia excretion rate, nmol N *ind.*$^{-1}$ h^{-1}), NH4+ ex. rt. (DM) (Temperature corrected–ammonia excretion rate, nmol N mg *DM*$^{-1}$ h^{-1}), PO43- ex. rt. (ind.) (Temperature corrected–phosphate excretion rate, nmol P *ind.*$^{-1}$ h^{-1}), PO43- ex. rt. (DM) (Temperature corrected–phosphate excretion rate, nmol N mg *DM*$^{-1}$ h^{-1}), N:P excr. (N:P excretion ratio, molar); **NA : Not available (Not enough data for same species).**

ln (variables)	BL	DM	C ct	N ct	P ct	N:P body	Prot ct	Lipid ct	Resp. rt. (ind.)	Resp. rt. (DM)	NH_4^+ ex. rt. (ind.)	NH_4^+ ex. rt. (DM)	PO_4^{3-} ex. rt. (ind.)	PO_4^{3-} ex. rt. (DM)	N:P excr.
BL	-	(183)	(18)	(40)	(37)	(37)	(9)	(6)	(26)	(26)	(40)	(40)	(39)	(39)	(34)
DM	**0.90**	-	(46)	(105)	(65)	(66)	15)	(9)	(59)	(59)	(71)	(71)	(47)	(47)	(42)
C ct	-0.28	0.02	-	(46)	(46)	(46)	(7)	*NA*	(41)	(41)	(37)	(37)	(11)	(11)	(11)
N ct	-0.09	**-0.34**	**0.37**	-	(64)	(64)	(14)	(6)	(45)	(45)	(48)	(48)	(20)	(20)	(22)
P ct	**-0.37**	**-0.41**	**0.39**	-0.22	-	(66)	(10)	(4)	(46)	(46)	(42)	(42)	(17)	(17)	(17)
N:P body	0.08	**0.27**	-0.15	**0.60**	**-0.82**	-	(10)	(4)	(46)	(46)	(44)	(44)	(17)	(17)	(18)
Prot ct	0.05	-0.07	0.25	-0.23	0.32	-0.18	-	(5)	(7)	(7)	(13)	(13)	(11)	(11)	(11)
Lipid ct	0.65	0.24	*NA*	-0.31	-0.69	0.48	-0.85	-	*NA*	*NA*	(5)	(5)	(4)	(4)	(4)
Resp. rt. (ind.)	**0.68**	**0.70**	**0.33**	0.06	-0.08	0.01	0.01	*NA*	-	(59)	(37)	(37)	(13)	(13)	(12)
Resp. rt. (DM)	-0.34	**-0.35**	0.05	**0.33**	-0.14	0.13	-0.13	*NA*	**0.42**	-	(37)	(37)	(13)	(13)	(12)
NH_4^+ exc. (ind.)	**0.84**	**0.86**	0.15	0.07	-0.24	0.23	0.06	0.22	**0.86**	0.19	-	(71)	(42)	(42)	(40)
NH_4^+ exc. (DM)	**-0.60**	**-0.36**	0.28	**0.40**	**0.31**	-0.03	0.01	0.11	**0.44**	**0.65**	0.13	-	(42)	(42)	(40)
PO_4^{3-} exc. (ind.)	**0.78**	**0.85**	-0.41	0.18	**-0.68**	**0.61**	-0.01	0.33	0.18	-0.41	**0.92**	-0.29	-	(47)	(41)
PO_4^{3-} exc. (DM)	**-0.60**	**-0.65**	<0.01	0.39	**0.66**	-0.29	0.21	-0.87	-0.51	-0.12	**-0.38**	**0.76**	-0.20	-	(41)
N:P exc.	0.14	0.15	0.26	-0.24	-0.21	-0.13	-0.02	0.13	0.26	0.35	<0.01	-0.11	-0.18	**-0.46**	-

Table 3. Major axis regression equations, number of species included (*N*), Pearson correlation coefficients (*r*), coefficients of determination (R^2), and statistical significance (*P*) of mass-length allometric relationships for different subsets of species from the database, grouped based on either major habitat and/or taxa. *DM* corresponds to body dry mass (mg) and *L* to body length (mm) of species.

Figure Index‡	Subset of Species	Regression Equations	*N*	*r*	R^2	*P*
	All species					
2a		ln DM = 2.829 ln L – 4.517	183	0.90	0.80	<0.001
	Species according to major habitats					
2b	Marine Species	ln DM = 2.791 ln L – 3.910	37	0.97	0.94	<0.001
2b	Freshwater Species	ln DM = 2.075 ln L – 4.814	148	0.86	0.74	<0.001
	Species according to taxa					
2c-i	Calanoida	ln DM = 3.469 ln L – 4.729	58	0.90	0.80	<0.001
2c-ii	Cyclopoida	ln DM = 2.713 ln L – 4.894	39	0.89	0.80	<0.001
2c-iii	Daphniids	ln DM = 2.735 ln L – 5.043	34	0.91	0.82	<0.001
2c-iv	Cladocera (Other than Daphniids)	ln DM = 1.907 ln L – 4.589	51	0.84	0.70	<0.001
	Species according to major habitat and taxa					
-	Freshwater Calanoida	ln DM = 2.880 ln L – 5.140	25	0.62	0.39	<0.001
-	Marine Calanoida	ln DM = 2.647 ln L – 3.771	33	0.97	0.94	<0.001
-	Freshwater Cyclopoida	ln DM = 2.747 ln L – 4.984	36	0.93	0.86	<0.001
-	Marine Cyclopoida	ln DM = 2.782 ln L – 3.811	3	0.97	0.94	NS

‡ Letters indicate the corresponding panel in figure 2; for panel 2b, roman numerals represent the corresponding fitted lines.

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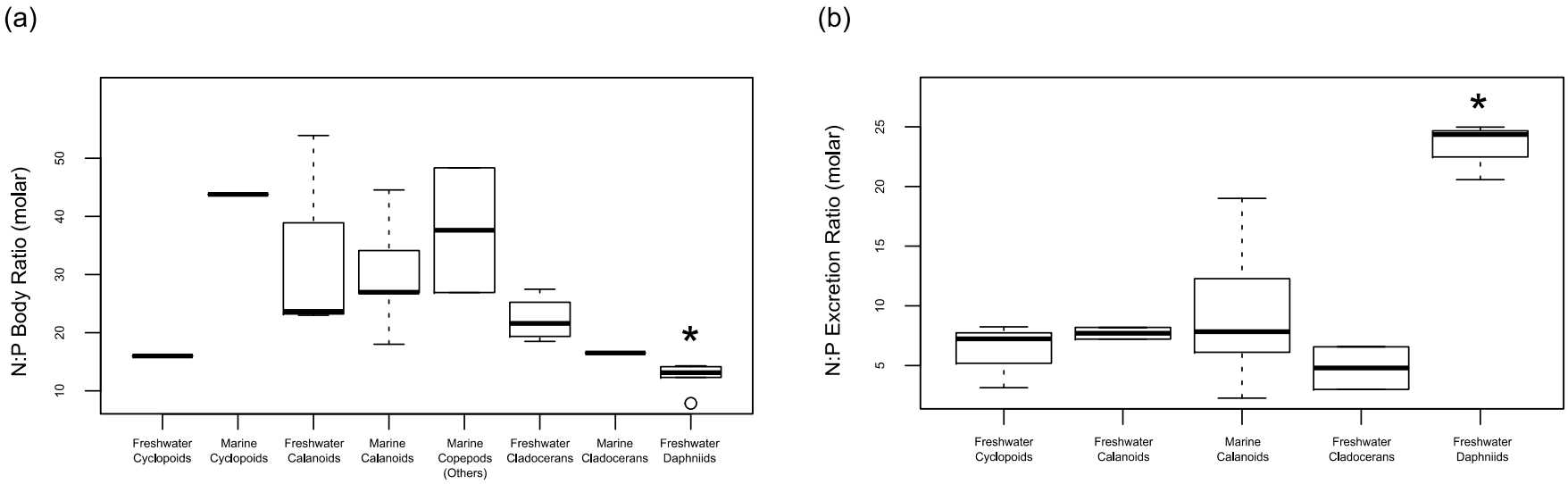

Figure 1. Box-plots representing the data variability of N:P body ratio (a) and N:P excretion ratio (b) among zooplankton species groups based on taxa and habitat. The solid horizontal line within each box indicates the median value for the taxon. Box boundaries represent the lower and upper quartiles. Whisker extents represent the 10th and 90th percentiles. Dots correspond to species' trait values falling outside the 10th and 90th percentiles. The symbol * indicates that daphniid species exhibit trait values significantly different from other taxa. Box-plots are based on raw data (i.e. prior to ln-transformation). Outliers are removed in order to compare medians and quartiles among groups.

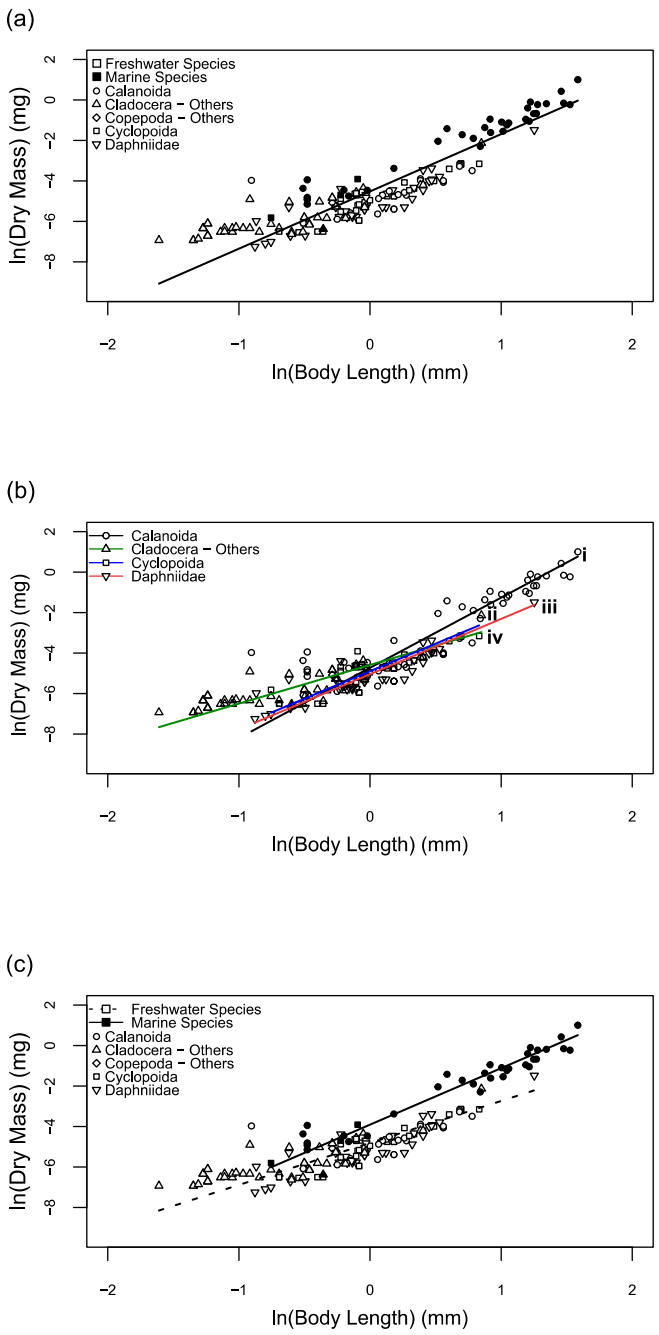

Figure 2. Regressions by major axis of mass-length allometric relationships. Each point represents a species mean. Each taxonomic group is represented by a different symbol; the color of the symbol indicates the type of habitat to which species belong. Regressions were performed on (a) overall species, (b) among main taxa and (c) between major habitats. For panel b, roman numerals (i, ii, iii and iv) represent the corresponding fitted lines: Calanoida, Cyclopoida, Daphniids and Cladocera (other than daphniids). All outliers and observations on non-adult or male individuals were previously removed.

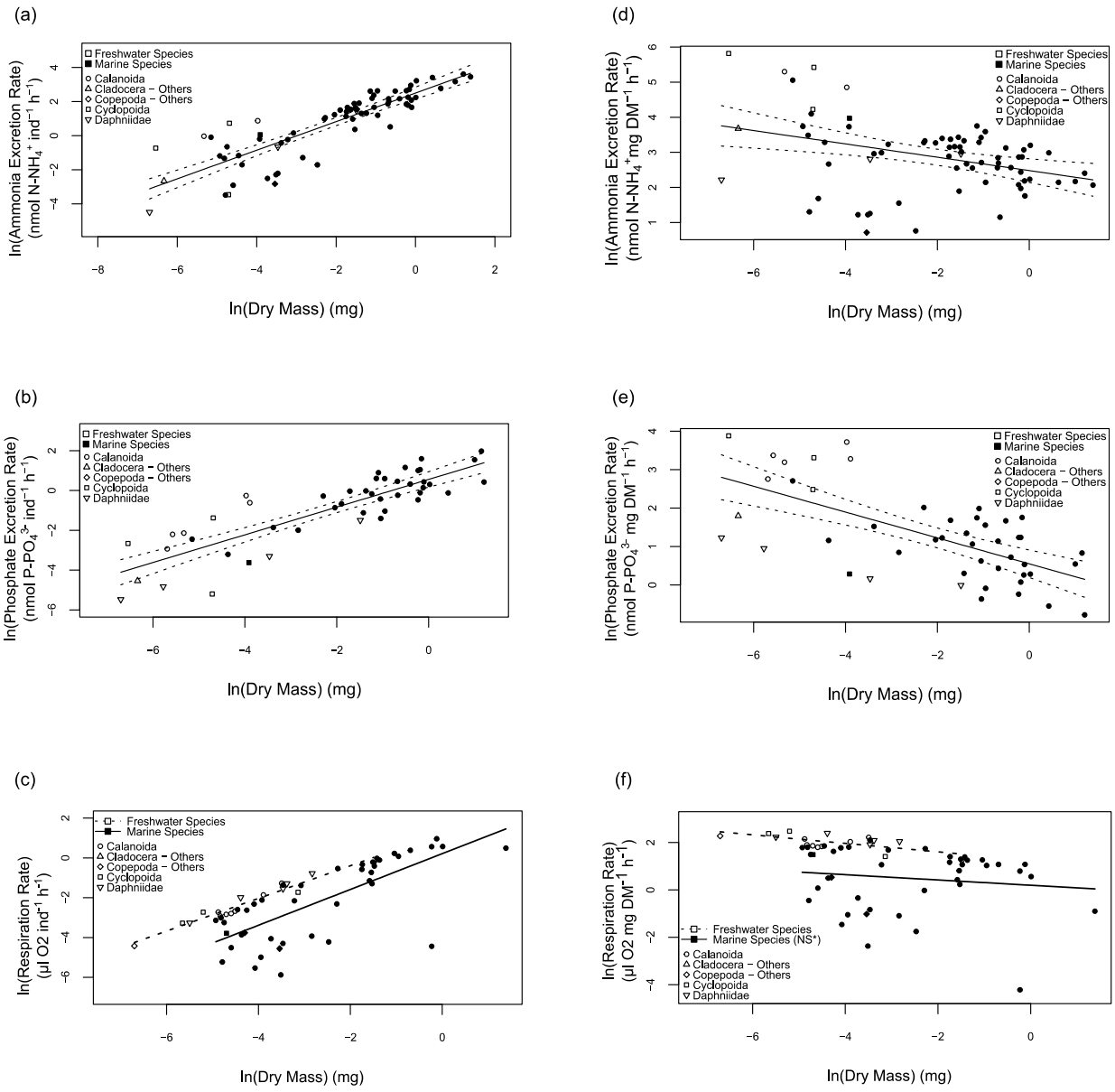

Figure 3. Regressions (OLS) of excretion and respiration rates as a function of species body mass. Ammonia and phosphate excretion rates and respiration rates are expressed both per individual (a, b, c) and per unit dry mass (d, e, f). Each point represents a species mean. Each taxonomic group is represented by a different symbol; the color of the symbol indicates the type of habitat to which species belong. For panels a-d, dotted lines represent the 95% confidence interval for the best-fit line (all significant at $p < 0.0001$). For panels e and f, the confidence interval is not provided; dotted line represents the best-fit line for freshwater species and the solid line represents the best-fit line for marine species. All outliers and observations on non-adult or male individuals were previously removed.

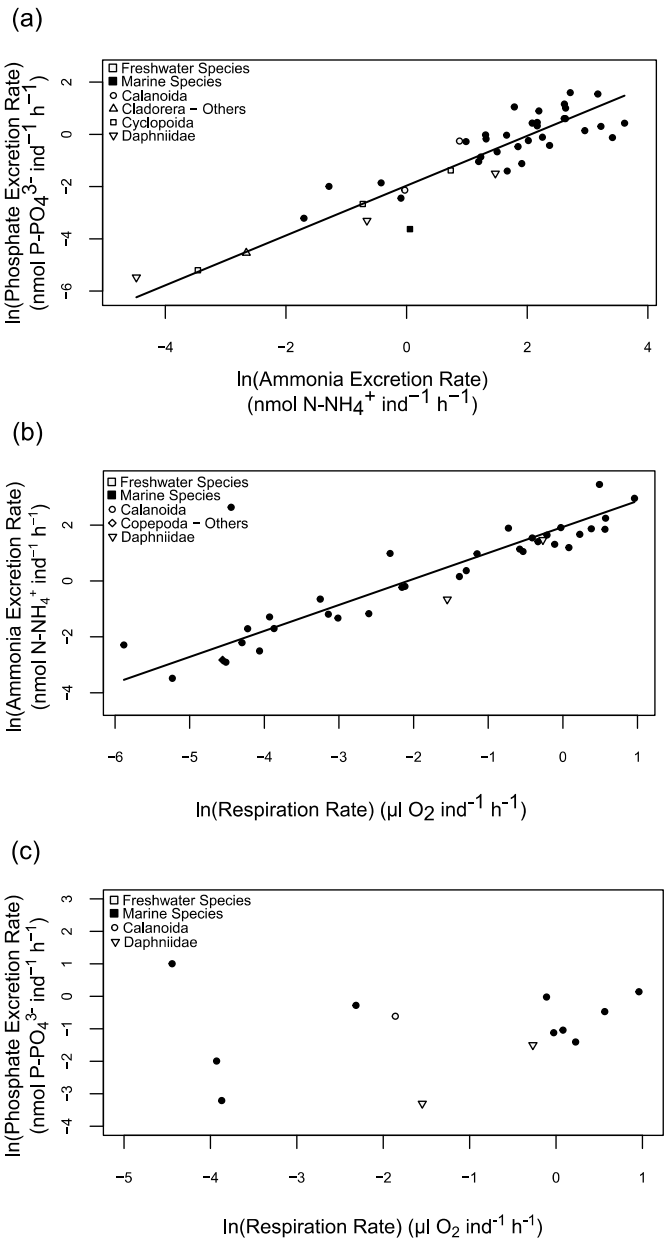

Figure 4. Regressions by major axis between physiological traits: N excretion versus P excretion rates (a), N and P excretion versus respiration rates (b, c). Each point represents a species mean. Each taxonomic group is represented by a different symbol; the color of the symbol indicates the type of habitat to which species belong. All outliers and observations on non-adult or male individuals were previously removed.

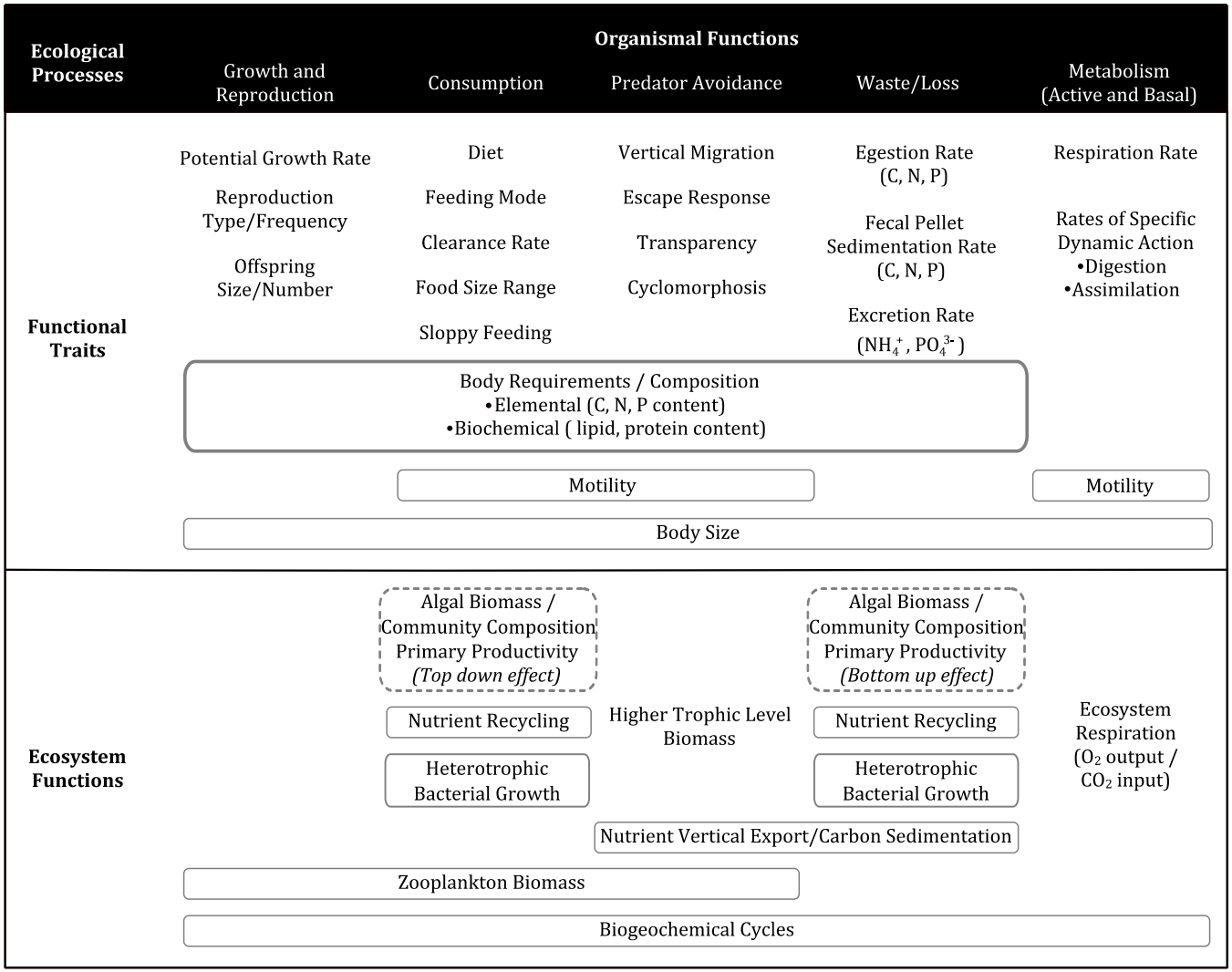

Figure 5a. A non-exhaustive classification of zooplankton functional traits based on the energy budget of an organism (organismal functions) and on their respective impact on ecosystem (ecosystem functions). Traits and ecosystem functions that transcend more than one organismal function are framed with solid lines. Larger frames at the bottom may encompass other traits listed above. Frames with dotted lines indicate the bidirectional control (top down and bottom up) on the algal communities. This scheme has been partly inspired by Litchman *et al.,* 2013.

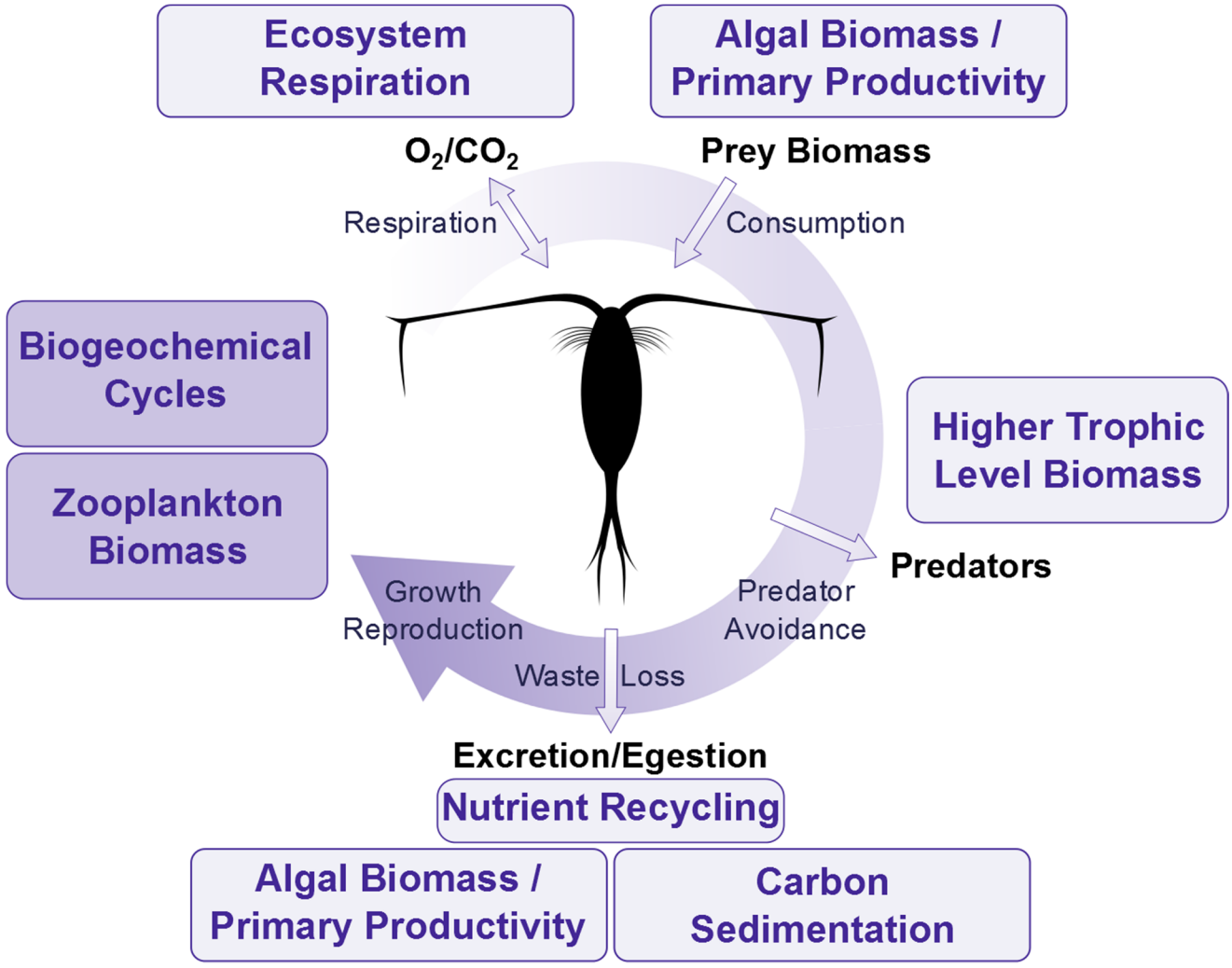

Figure 5b. Typical interactions of a zooplankter with its environment, in terms of direct chemical output, input or energy transfer. Items in bold indicate the organism from, or to which, there will be a transfer of energy, and the type of product released or uptaken by an herbivorous calanoid. Organismal functions regulating these exchanges are indicated next to the small arrows. Boxes denote the ecosystem functions that are influenced by these interactions. All organismal functions contribute to the overall goal of "Growth and Reproduction", which influences zooplankton biomass in the system directly, and modulates biogeochemical cycles indirectly – this concept is represented by the circular arrow. Note that figure 5b does not include all ecosystem processes listed in figure 5a.

Chapitre 3 : Conclusions générales

La présente étude a permis d'améliorer notre compréhension globale de la structure de communauté des crustacés zooplanctoniques en faisant la revue et l'analyse quantitative des données empiriques de traits influençant les cycles de N, P et C à travers les écosystèmes. Notre recherche a donné fruit à une base de données comprenant plus de 9000 observations portant respectivement sur 134 et 153 espèces marines et dulcicoles. L'approche par trait utilisée dans notre analyse a entre autres permis de quantifier les relations entre les traits et de détecter la présence de patrons entre les grands groupes taxonomiques et les principaux habitats aquatiques. Caractériser ces relations permettra de mieux prédire la contribution des espèces aux processus écosystémiques, selon les groupes taxonomiques présents et le type d'habitat dans lequel ceux-ci se retrouvent. De plus, les coefficients de corrélation et les équations de régression présentés obtenus par ce travail permettront d'estimer les valeurs de traits pouvant être plus difficiles, ou coûteux, à mesurer à partir de traits plus accessibles. Ainsi, nos modèles facilitent et encouragent l'incorporation des traits physiologiques dans la caractérisation de communauté se basant sur les assemblages de traits.

Certaines des relations que nous avons observées ont su confirmer les tendances déjà connues, notamment l'équilibre stœchiométrique entre les besoins corporels et la quantité de nutriments excrété de même que la tendance d'un ratio N:P généralement inférieur à 16 dans l'excrétion du zooplancton. Cependant, notre étude à grande échelle a mis en évidence une différence significative entre les espèces marines et dulcicoles pour

ce qui de (1) leurs taux métaboliques moyens (respiration, excrétion de N et de P), (2) la relation entre la masse et la longueur corporelle, puis (3) la relation entre la respiration spécifique et la masse des organismes. La taille des espèces marines étant en moyenne plus élevée que celles des espèces en eaux douces, les taux de respiration et d'excrétion par individu étaient tous plus élevés pour le zooplancton marin, mais une fois rapportés par unité de masse sèche, ces taux étaient tous plus faibles que ceux présentés par les espèces d'eaux douces. Ceci implique qu'à biomasse équivalente, le zooplancton d'eaux douces contribue de façon relativement plus importante aux flux d'éléments de son système. Nous avons de plus montré que les espèces marines présentaient une masse corporelle plus élevée que les espèces dulcicoles ayant une longueur de taille équivalente et que les espèces en eaux douces respiraient en moyenne à un taux trois fois plus élevé que les espèces océaniques. Considérant que ces patrons étaient tous significativement plus différents entre les habitats qu'entre les groupes taxonomiques, nos résultats suggèrent que ces traits seraient susceptibles d'être influencés par la variabilité environnementale. La différence au niveau de l'allométrie et de la respiration spécifique entre les espèces des systèmes marins et dulcicoles pourrait entre autres résulter de stratégies écologiques ayant différemment évolué selon les contraintes du milieu. Il n'en demeure pas moins que ces différences présentent des implications potentiellement importantes pour les flux et l'emmagasinage de carbone en milieu aquatique, que ce soit en termes d'émission de CO_2 ou le lot d'énergie stocké dans les tissus du zooplancton.

L'objectif final de notre étude était d'établir un cadre de travail intégrateur afin de catégoriser les traits fonctionnels du zooplancton en vue de mieux lier les espèces aux

processus écosystémiques qu'ils affectent. L'approche hiérarchique de notre classification identifie les traits répondant aux différentes fonctions individuelles des organismes et les lie aux fonctions écosystémiques qu'ils peuvent influencer. Nous espérons que cette contribution saura assister les écologistes dans le choix des traits pour la caractérisation des communautés de zooplancton et stimulera l'intégration entre les champs de l'écologie des communautés et de la biogéochimie.

Bien que nous soyons confiants quant aux patrons révélés par notre analyse synthétique, notre base de données présente certaines limitations contraignant nos analyses statistiques, tel que le nombre d'observation variant entre les traits, les taxa ou les habitats. Cette situation est toutefois fréquente pour les méta-analyses en écologie, particulièrement lorsque les études sont menées à grande échelle (Koricheva *et al.*, 2013). Par ailleurs, nous espérons que plus de données phylogénétiques sur les espèces de zooplancton seront disponibles dans le futur afin de pouvoir prendre en considération la variabilité génétique entre les espèces dans nos analyses. En effet, bien que nous ayons exploré les différences entre les valeurs de traits de différents taxa, l'utilisation de méthodes de comparaison phylogénétique (Felsenstein, 1985), notamment les modèles phylogénétiques par moindre des carrés généralisés (PGLS; Freckleton *et al*., 2002) ou les cartes de vecteurs propres phylogénétiques (Guénard *et al*., 2013), pourraient améliorer la robustesse de nos modèles (Freckleton, 2009). Les distances phylogénétiques entre les espèces pourraient effectivement être utilisées afin d'inférer les valeurs de trait manquantes pour certaines espèces, ce qui pourrait ainsi augmenter le nombre d'observations de nos modèles. Ceci étant dit, pour que ce type d'inférence fonctionne et

puisse adéquatement représenter la distribution des valeurs de traits entre les espèces, le nombre de valeurs à combler doit être relativement faible (Guénard *et al.*, 2011). Cependant, tel que démontré dans notre étude, certaines valeurs de traits n'ont pas encore été mesurées pour plusieurs espèces, particulièrement celles en milieux d'eaux douces. Néanmoins, nous espérons qu'en ayant fait le point sur la disponibilité des données dans la littérature, notre étude saura diriger les efforts de recherches à venir et stimulera la mesure et l'usage des traits physiologiques dans les classifications fonctionnelles.

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Annexe: Supplément pour le chapitre 2

Table A.I. List of zooplankton species associated to trait values considered as statistical outliers in the present study. All respiration and excretion rates ranges are standardized for temperature (*).

	Trait	Value (unit)
Marine Species		
Acanthodiaptomus sp.	Respiration rate	5.29 (µL O_2 ind^{-1} h^{-1})*
Acartia sp.	Specific ammonia excretion rate	157.0 (nmol N-NH_4^+ DM^{-1} h^{-1})*
Calanus finmarchicus	C content	55.5 (%)
Calanus hyperboreus	Body length	6.65 (mm)
	C content	62.4 (%)
	N content	17.0 (%)
	P content	4.38 (%)
	Lipid	74 (%)
Euchaeta antarctica	Body length	7.9 (mm)
Euchaeta norvegica	Individual ammonia excretion rate	123.7 (nmol N-NH_4^+ ind^{-1} h^{-1})*
Gaussia princeps	Dry mass	7 (mg)
Metridia pacifica	C content	53.9 (%)
	N :P body ratio	0.34 (%)
Neocalanus plumcrus	Protein content	10.9 (%)
	Respiration rate	3.04 (µL O_2 ind^{-1} h^{-1})*
Paraeuchaeta brevirostris	Dry mass	4.97 (mg)
Paraeuchaeta elongata	N content	37.5 (%)
Paraeuchaeta orientalis	Dry mass	8.56 (mg)
Spinocalanus antarcticus	N content	4.75 (%)
Freshwater Species		
Alonella nana	Dry mass	0.00098 (mg)
Bythotrephes longimanus	Body length	12 (mm)
Leptodiaptomus siciloides	Specific ammonia excretion rate	200.0 (nmol N-NH_4^+ DM^{-1} h^{-1})*
Leptodora kindtii	Body length	15.8 (mm)
	Dry mass	0.009 (mg)
Limnocalanus macrurus	C content	63 (%)
	N content	5.3 (%)
Mesocyclops leuckarti	Specific ammonia excretion rate	225.7 (nmol N-NH_4^+ DM^{-1} h^{-1})*
Mixodiaptomus laciniatus	P content	4.66 (%)
	N content	50.4 (%)

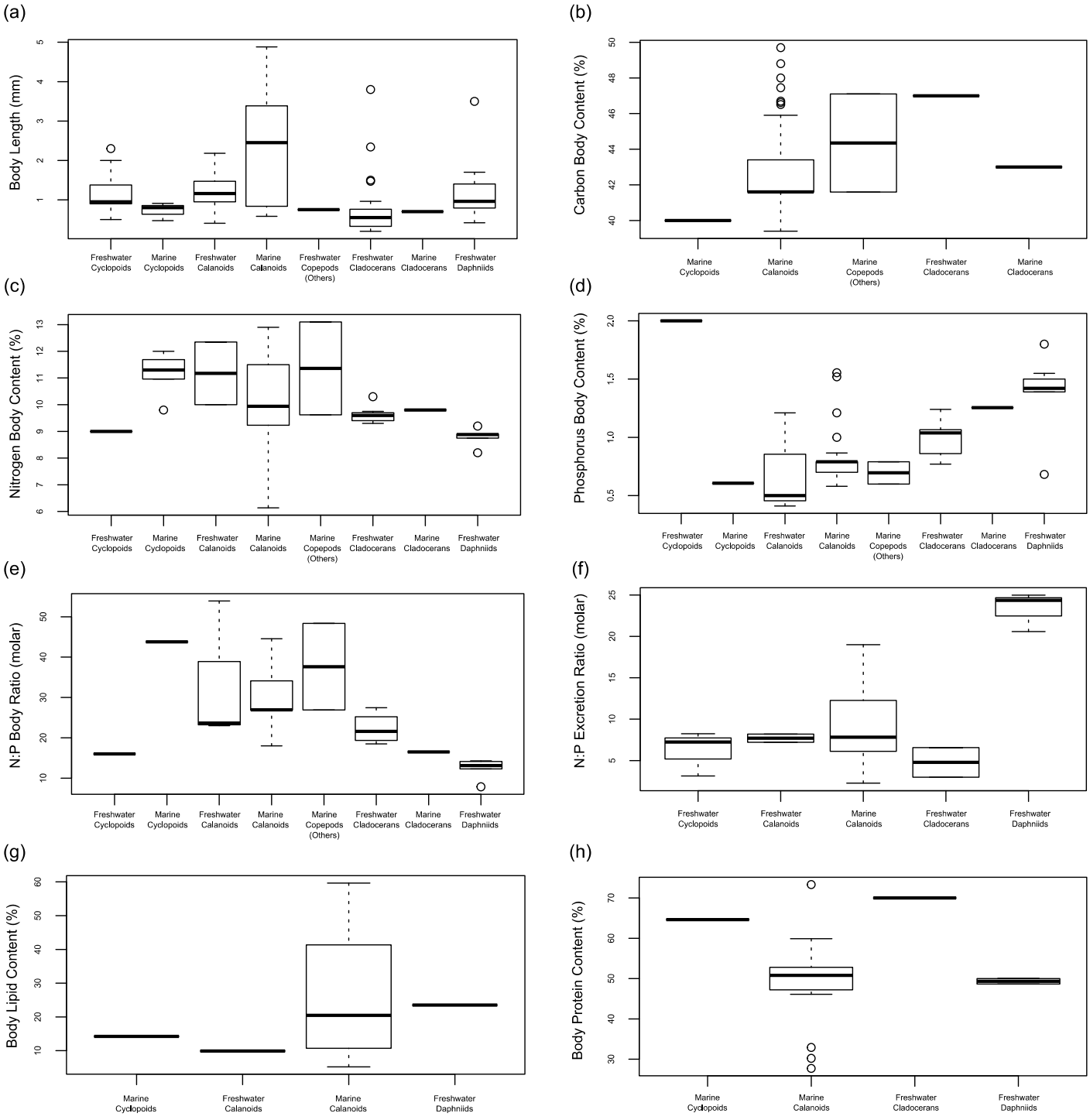
Table A.II. List of freshwater and marine zooplankton species included in the present meta-analysis. All observations on reported on male or non-adult species do not appear in this list.

Freshwater Species	**Marine Species**
Acanthocyclops robustus	*Acanthodiaptomus* sp.
Acanthocyclops vernalis	*Acartia australis*
Acantholeberis curvirostris	*Acartia clausi*
Acroperus harpae	*Acartia lilljeborgi*
Alona affinis	*Acartia longiremis*
Alona costata	*Acartia pacifica*
Alona guttata	*Acartia spinicauda*
Alona quadrangularis	*Acartia tonsa*
Alona sp.	*Acartia* sp.
Alonella acutirostris	*Acrocalanus gibber*
Alonella nana	*Amallothrix valida*
Alonella sp.	*Anomalocera patersoni*
Arctodiaptomus dorsalis	*Arietellus plumifer*
Boeckella delicata	*Calanopia elliptica*
Bosmina freyi	*Calanus chilensis*
Bosmina liederi	*Calanus cristatus*
Bosmina liederi/longirostris	*Calanus finmarchicus*
Bosmina longirostris	*Calanus glacialis*
Bosmina longispina mantima	*Calanus helgolandicus*
Bosmina sp.	*Calanus lighti*
Bosmina tubicens	*Calanus pacificus*
Bosminopsis deitersi	*Calanus plumchrus*
Bythotrephes longimanus	*Calanus propinquus*
Calamoecia lucasi	*Calanus propinquus*
Camptocercus sp.	*Calanus robustior*
Canthocamptus staphylinus	*Calanus* sp.
Ceriodaphnia lacustris	*Candacia aethiopica*
Ceriodaphnia megalops	*Candacia aetiopica*
Ceriodaphnia pulchella	*Candacia armata*
Ceriodaphnia quadrangula	*Candacia columbiae*
Ceriodaphnia reticulata	*Candacia pachydactyla*
Ceriodaphnia rigaudi	*Centropages abdominaris*
Ceriopdaphnia sp.	*Centropages brachiatus*
Chydorus bicornutus	*Centropages spp.*
Chydorus faviformis	*Centropages typicus*

Chydorus sp.
Chydorus sphaericus
Cyclopoida sp.
Cyclops abyssorum
Cyclops bicuspidatus
Cyclops bohater
Cyclops kolensis
Cyclops leuckarti
Cyclops scutifer
Cyclops strenuus
Cyclops vernalis
Cyclops vicinus
Daphnia ambigua
Daphnia catawba
Daphnia cucullata
Daphnia cucullata x galeata
Daphnia dentifera
Daphnia dubia
Daphnia galeata mendotae
Daphnia hyalina
Daphnia hyalina x galeata
Daphnia laevis
Daphnia longiremis
Daphnia longispina
Daphnia lumholtzi
Daphnia magna
Daphnia minnehaha
Daphnia parvula
Daphnia pulex
Daphnia pulicaria
Daphnia retrocurva
Daphnia rosea
Daphnia schoedleri
Daphnia sp.
Daphnia thorata
Diacyclops bicupidatus thomasi
Diacyclops sp.
Diaphanosoma birgei
Diaphanosoma brachyurum
Diaphanosoma leuchtenbergianum
Diaphanosoma sp.
Chiridius armatus
Chiridius pacificus
Chirundina streetsi
Corycaeus sp.
Cyclopina longicornis
Disseta palumboi
Eucalanus attenuatus
Eucalanus bungii
Eucalanus californius
Eucalanus subcrassus
Euchaeta elongata
Euchaeta flava
Euchaeta marina
Euchaeta norvegica
Euchaeta spinosa
Eucheata acuta
Euchirella bitumida
Euchirella brevis
Euchirella galeata
Euchirella intermedia
Euchirella messinensis
Euchirella rostrata
Euchirella sp.
Euchirella truncata
Eurytemora affinis
Euterpina acutifrons
Evadne nordmanni
Gaetanus paracurvicornis
Gaidius variabilis
Gaussia princeps
Labidocera actifrons
Labidocera acuta
Labidocera fluvialitis
Labidocera nerii
Labidocera sp.
Macrosetella sp.
Megacalanus princeps
Mesocalanus tenuicornis
Metridia asymmetrica
Metridia curticauda
Metridia gerlachei

Diaptomid copepodas
Diaptomus dorsalis
Diaptomus floridanus
Diaptomus gracilis
Diaptomus graciloides
Diaptomus leptopus
Diaptomus leptopus
Diaptomus minutus
Diaptomus oregonensis
Diaptomus siciloides
Disparalona acutirostris
Epischura lacustris
Epischura sp.
Eubosmina coregoni
Eucyclops agilis
Eucyclops elegans
Eucyclops neomacruroides
Eucyclops serrulatus
Eucyclops sp.
Eucyclops speratus
Eudiaptomus gracilis
Eurycercus sp.
Eurytemora sp.
Eurytemora velox
Holopedium amazonicum
Holopedium gibberum
Holopedium sp.
Ilyocryptus sp.
Latona setifera
Latona sp.
Leptodiaptomus ashlandi
Leptodiaptomus minutus
Leptodiaptomus sicilis
Leptodiaptomus siciloides
Leptodora sp.
Leydigia acanthocercoides
Leydigia sp.
Limnocalanus macrurus
Macrocyclops albidus
Macrocyclops sp.
Macrothrix laticornis
Metridia longa
Metridia okhotensis
Nannocalanus minor
Neocalanus cristatus
Neocalanus gracilis
Neocalanus plumcrus
Neocalanus robustior
Oithona atlantica
Oithona hebes
Oithona oswaldocruzi
Oithona similis
Oncaea venusta
Paracalanus aculeatus
Paracalanus parvus
Paracalanus sp.
Paraeuchaeta barbata
Paraeuchaeta birostrata
Paraeuchaeta brevirostris
Paraeuchaeta elongata
Paraeuchaeta modesta
Paraeuchaeta orientalis
Paraeuchaeta pseudotumidula
Paraeuchaeta rubra
Paraeuchaeta sarsi
Pleuromamma abdominalis
Pleuromamma robusta
Pleuromamma scutullata
Pleuromamma sp.
Pleuromamma xiphias
Pontella atlantica
Pontella danae
Pontella fera
Pontella sp.
Pontellina plumata
Pseudocalanus elongatus
Pseudocalanus minutus elongatus
Pseudodiaptomus acutus
Pseudodiaptomus marinus
Rhincalanus cornutus
Rhincalanus gigas
Rhincalanus nasutus

Macrothrix rosea
Macrothrix sp.
Megacyclops gigas
Megacyclops viridis
Mesocyclops edax
Mesocyclops leuckarti
Mesocyclops sp.
Mixodiaptomus laciniatus
Moina sp.
Orthocyclops modestus
Orthocyclops sp.
Paracyclops sp.
Paralona pigra
Pleuroxus procurvus
Pleuroxus sp.
Polyphemus pediculus
Polyphemus sp.
Pseudochydorus
Scapholeberis sp.
Senecella calanoidaes
Sida crystallina
Sida sp.
Simocephalus exspinosus
Simocephalus serrulatus
Simocephalus sp.
Simocephalus vetulus
Skistodiaptomus oregonensis
Skistodiaptomus pallidus
Skistodiaptomus sp.
Thermocyclops crassus
Thermocyclops hyalinus
Thermocyclops oithonoides
Tropocyclops extensus
Tropocyclops prasinus
Tropocyclops prasinus mexicanus
Tropocyclops sp.
Rhincalanus rostrifrons
Scaphocalanus magnus
Scaphocalanus medius
Scolecithricella sp.
Scolecithrix bradyi
Scottocalanus securifrons
Spinocalanus stellatus
Temora discaudata
Temora turbinata
Tortanus discaudatus
Tortanus gracilis
Undeuchaeta incisa
Undeuchaeta itnermedia
Undeuchaeta major
Undeuchaeta plumosa
Undinula darwinii
Undinula vulgaris


(a)
Body Length (mm)
Freshwater Cyclopoids
Marine Cyclopoids
Freshwater Calanoids
Marine Calanoids
Freshwater Copepods (Others)
Freshwater Cladocerans
Marine Cladocerans
Freshwater Daphniids
(b)
Carbon Body Content (%)
Marine Cyclopoids
Marine Calanoids
Marine Copepods (Others)
Freshwater Cladocerans
Marine Cladocerans
(c)
Nitrogen Body Content (%)
(d)
Phosphorus Body Content (%)
(e)
N:P Body Ratio (molar)
(f)
N:P Excretion Ratio (molar)
(g)
Body Lipid Content (%)
(h)
Body Protein Content (%)

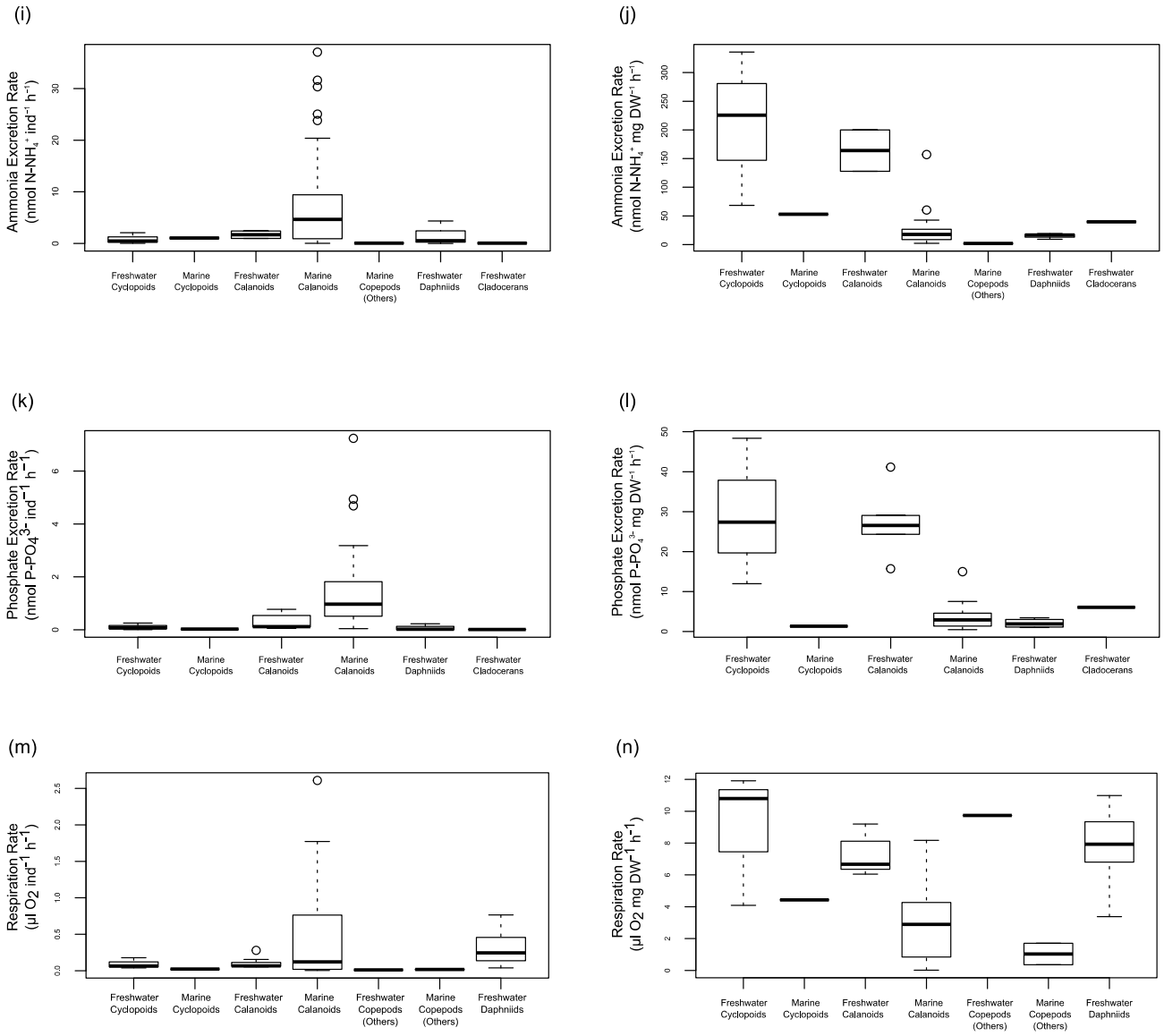
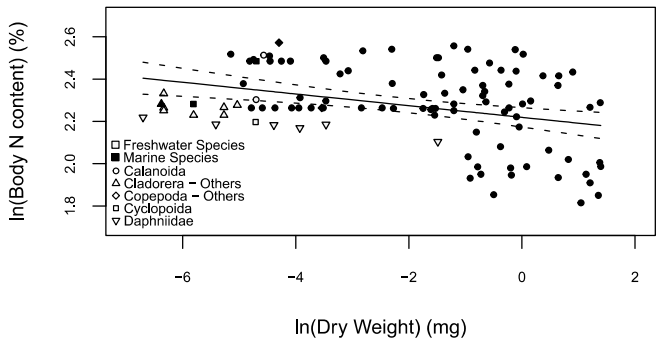
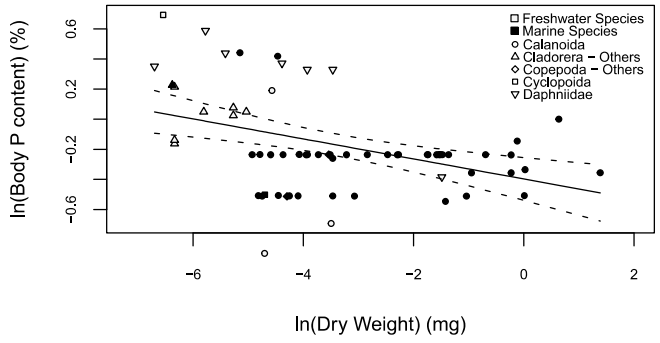


Figure A.I. Box-plots representing the distribution of trait values among among zooplankton species groups based on taxa and habitat. The solid horizontal line within each box indicates the median value for the taxon. Box boundaries represent the lower and upper quartiles. Whisker extents represent the 10th and 90th percentiles. Dots correspond to species' trait values falling outside the 10th and 90th percentiles. Box-plots were performed on raw data (i.e. prior to ln-transformation). Outliers were previously removed in order to compare medians and quartiles among groups.

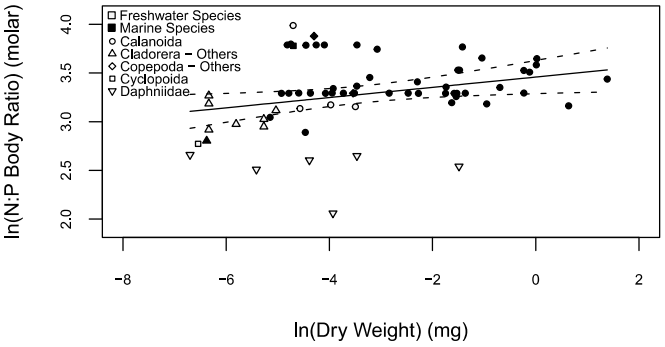
(a)


ln(Body N content) (%)
1.8
2.0
2.2
2.4
2.6
Freshwater Species
Marine Species
Calanoida
Cladorera – Others
Copepoda – Others
Cyclopoida
Daphniidae
−6
−4
−2
0
2
ln(Dry Weight) (mg)

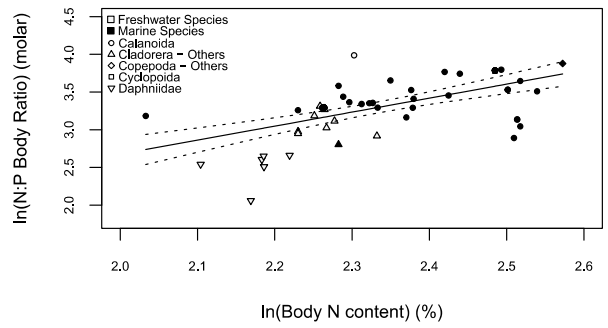
(b)


ln(Body P content) (%)
−0.6
−0.2
0.2
0.6
Freshwater Species
Marine Species
Calanoida
Cladorera – Others
Copepoda – Others
Cyclopoida
Daphniidae
−6
−4
−2
0
2
ln(Dry Weight) (mg)

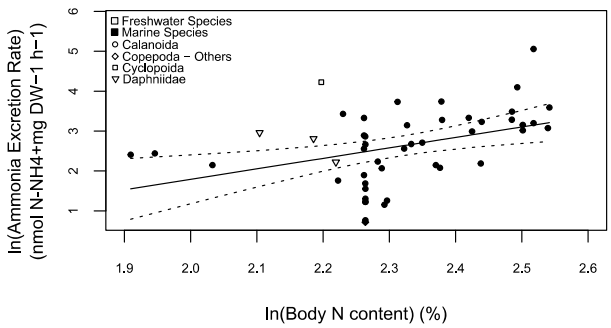
(c)


ln(N:P Body Ratio) (molar)
2.0
2.5
3.0
3.5
4.0
Freshwater Species
Marine Species
Calanoida
Cladorera – Others
Copepoda – Others
Cyclopoida
Daphniidae
−8
−6
−4
−2
0
2
ln(Dry Weight) (mg)

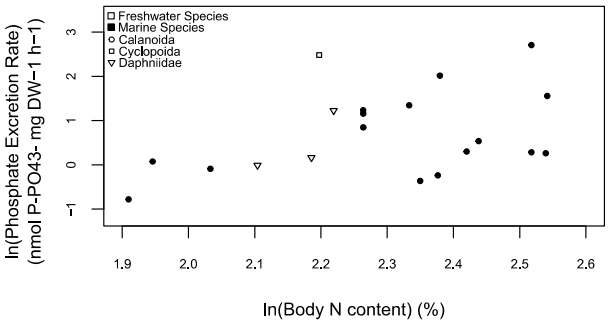
(d)


Freshwater Species
Marine Species
Calanoida
Cladorera – Others
Copepoda – Others
Cyclopoida
Daphniidae
ln(N:P Body Ratio) (molar)
ln(Body N content) (%)

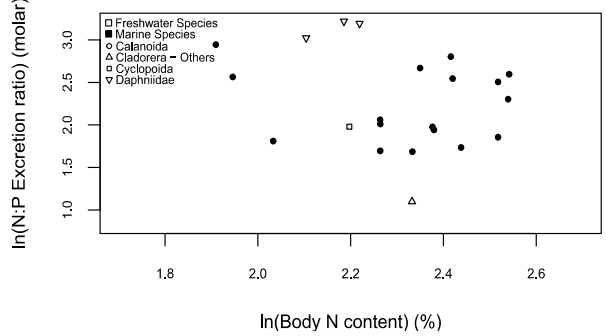
(e)


Freshwater Species
Marine Species
Calanoida
Copepoda – Others
Cyclopoida
Daphniidae
ln(Ammonia Excretion Rate)
(nmol N-NH4+mg DW−1 h−1)
ln(Body N content) (%)

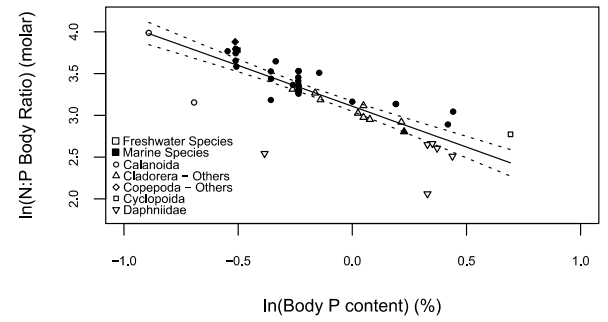
(f)


Freshwater Species
Marine Species
Calanoida
Cyclopoida
Daphniidae
ln(Phosphate Excretion Rate)
(nmol P-PO43- mg DW−1 h−1)
ln(Body N content) (%)

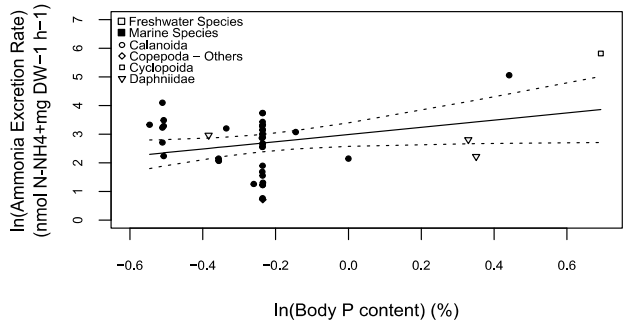
(g)


Freshwater Species
Marine Species
Calanoida
Cladorera – Others
Cyclopoida
Daphniidae
ln(N:P Excretion ratio) (molar)
ln(Body N content) (%)

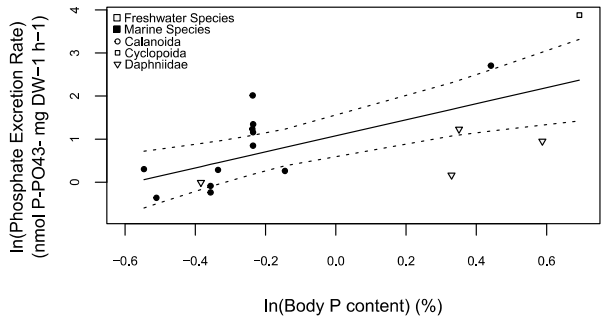
(h)


Freshwater Species
Marine Species
Calanoida
Cladorera – Others
Copepoda – Others
Cyclopoida
Daphniidae
ln(N:P Body Ratio) (molar)
ln(Body P content) (%)

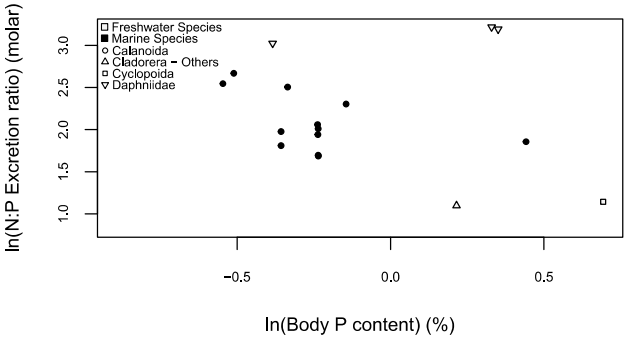
(i)


Freshwater Species
Marine Species
Calanoida
Copepoda – Others
Cyclopoida
Daphniidae
ln(Ammonia Excretion Rate)
(nmol N-NH4+mg DW−1 h−1)
ln(Body P content) (%)

(j)


Freshwater Species
Marine Species
Calanoida
Cyclopoida
Daphniidae
ln(Phosphate Excretion Rate)
(nmol P-PO43- mg DW−1 h−1)
ln(Body P content) (%)

(k)


Freshwater Species
Marine Species
Calanoida
Cladorera – Others
Cyclopoida
Daphniidae
ln(N:P Excretion ratio) (molar)
ln(Body P content) (%)

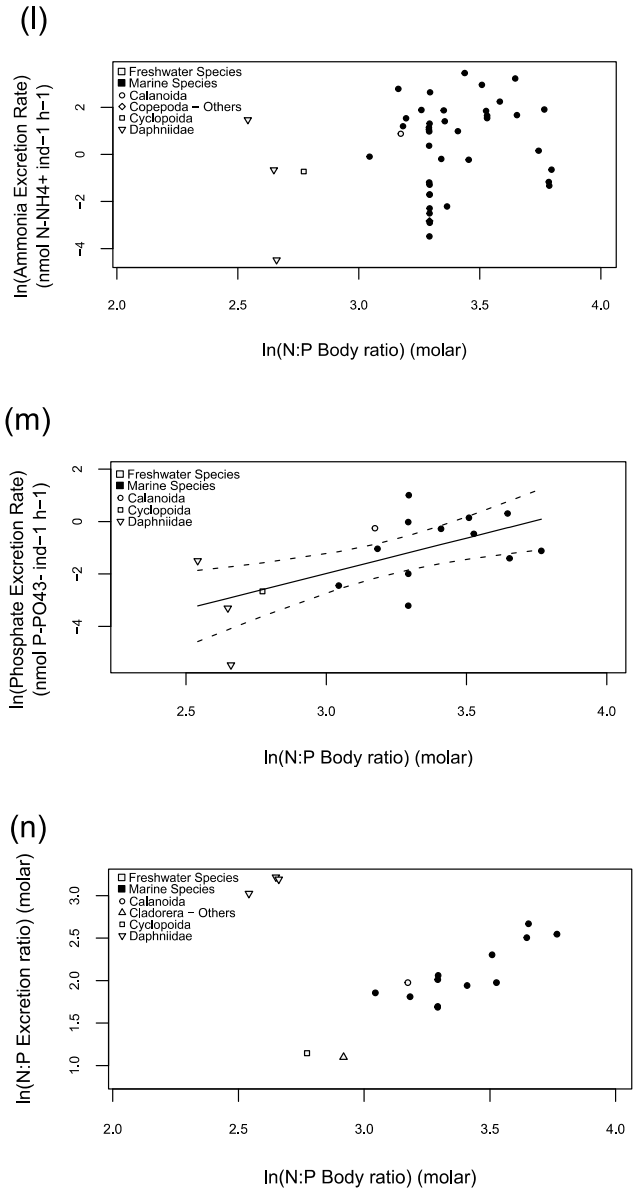


Figure A.II. Bivariate plots and regressions of body composition versus dry weight (a, b, c), N:P body ratio, excretion rates and ratio versus body N content (d, e, f, g), N:P body ratio, excretion rates and ratio versus body P content (h, I, j, k), and excretion rates and ratio versus N:P body ratio (l, m, n). Each point represents a species mean. Each taxonomic group is represented by a different symbol; the color of the symbol indicates the type of habitat to which species belong. Only lines with significant regression fits are indicated ($p<0.05$); dotted lines represent the 95% confidence interval for the best-fit line. All outliers (including ecologically-relevant outliers) are removed (see text for more details).

Descriptive Text for Fig. A.II

Elemental body composition in N and P was related to dry mass ($R^2_{adj.}$=0.11, n=105, $p < 0.001$ and $R^2_{adj.}$=0.16, n=67, $p < 0.001$, respectively) (Figs A.II a, b). The relationship for N:P body ratio versus dry mass was less apparent, although still statistically-significant at $p < 0.05$ ($R^2_{adj.}$=0.06, n=66) (Fig. A.II c). The relationship between elemental composition and body mass appears to be mainly driven by the type of habitat (Figs A.II a, b, c). However taxon also appears to play a role, likely related to the general trend of heavy mass- and (mostly) copepod species in marine habitats and lighter mass with more abundant cladoceran species in freshwater environments. Indeed, marine species (mostly copepods) were found to have higher N:P body ratio (Figs A. IId, h). Furthermore, N:P body ratio appeared to be better predicted by P body content ($R^2_{adj.}$=0.66, n=66, $p < 0.0001$) than by N body content ($R^2_{adj.}$=0.35, n=64, $p < 0.0001$), likely because of the wider variation in N content (Table 1, Figs A.II d, h).

As mentioned in results and discussion, relationships between body composition and excretion (rates and N:P ratio) were not always discernible, nor coherent (Figs A.II e-g, A.II i-n; Table 3). Specific N excretion rates were positively related to both N and P body content ($p < 0.05$) (Figs A.II e, i; Table 3), but there was no relationship with N:P body ratio (Fig. A.II l; Table 3). Specific P excretion rates were positively related to both P body content and N:P body ratio ($p < 0.05$) (Figs A.II j, m; Table 3), but there was no relationship with N body content (Fig. A.II f; Table 3). No trend was found between N:P excretion ratio versus N:P body ratio or N and P body content (Figs A.II g, k, n; Table 3).